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DEB or not to DEB, this is a question: comparison and analysis of the two population consequences of disturbance models: iPCoD EE and iPCoD DEB

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Glossary of Acronyms and Abbreviations

Term	Description
ABC	Approximate Bayesian Computation. A statistical method used to estimate parameter distributions when likelihood functions are difficult to compute.
DEB	Dynamic Energy Budget. A mechanistic bioenergetics modelling framework describing how organisms acquire and allocate energy for maintenance, growth, reproduction, and survival.
DD	Density Dependence. A process in which population growth rates change as population size changes due to competition for resources.
EE	Expert Elicitation. A structured process in which expert judgement is used to estimate relationships or parameters when empirical data are limited.
Env. Stoch.	Environmental Stochasticity. Random variation in environmental conditions affecting survival and reproduction in iPCoD EE and affecting resource availability in iPCoD DEB
HP	Harbour Porpoise (<i>Phocoena phocoena</i>).
HPDD	Harbour Porpoise Disturbance Days. The sum of the number of disturbed harbour porpoises over the days of offshore construction activities.
iPCoD	Interim Population Consequences of Disturbance. A modelling framework used to evaluate population-level effects of disturbance on marine mammals.
iPCoD DEB	Version of the iPCoD model where disturbance effects on vital rates are derived from a Dynamic Energy Budget bioenergetics model.
iPCoD EE	Version of the iPCoD model where disturbance effects on vital rates are derived from expert elicitation.
KEC	Kader Ecologie en Cumulatie (Ecological Framework for Cumulative Effects), a Dutch regulatory framework used to assess cumulative ecological impacts of offshore wind development.

1 Executive Summary

This report presents the results of a study commissioned by Rijkswaterstaat and carried out jointly by SMRU Consulting and TNO, comparing two population-modelling frameworks used to assess the effects of offshore wind farm construction on harbour porpoises in the North Sea: iPCoD EE (parameterised through expert elicitation) and iPCoD DEB (parameterised through a dynamic energy budget model). The work was motivated by the divergence in predictions between these two models in the KEC 5.0 assessment, where iPCoD DEB

produced markedly smaller estimated effects of disturbance than iPCoD EE for the same scenarios. The aim of the study was to clarify when and why the two models produce different — or similar — estimates of stressor effects, to characterise the sensitivity of iPCoD DEB to its key configuration choices, and to provide a basis on which regulators, assessors and developers can interpret results from either model in the context of KEC 6.0 and future assessments.

A first major outcome — not originally an objective of the assignment — was the identification and correction of a critical bug in the version of iPCoD DEB used in KEC 5.0, in which only a small fraction of the intended piling-related disturbance events were applied. Once corrected, iPCoD DEB was further modified to use matched pairs of disturbed and undisturbed populations sharing the same stochastic environment within each iteration, aligning its counterfactual structure with that of iPCoD EE. This alignment makes a like-for-like comparison between the two models possible and allows the application of the same summary metrics (5th, 50th and 95th percentile differences between disturbed and undisturbed populations) to both models. Code performance was also substantially improved through vectorisation and restructuring of the simulation loop, reducing runtime by approximately 5–10 fold. Full details of the bug fixes and code optimisation are provided in Appendix A.

Comparison of the two models on the international KEC 5.0 piling scenario revealed that the two models produce broadly similar magnitudes of maximum population decline at the 5th percentile when iPCoD DEB is run in its baseline configuration (no density dependence, no environmental stochasticity): –19% in iPCoD EE and –22% in iPCoD DEB. However, they differ in two important respects. First, iPCoD EE shows an earlier onset of decline. Second, iPCoD EE shows almost no recovery once disturbance ceases, whereas iPCoD DEB produces clear recovery — even in the absence of density dependence — driven by a disturbance-induced shift in age structure that releases reproductive capacity once disturbance ends. When density dependence and environmental stochasticity are switched on in iPCoD DEB, predicted impacts are substantially smaller (post-disturbance 5th percentile: –2%; maximum 5th percentile over the simulation: –3%), reflecting the buffering and compensatory roles of these two processes.

Sensitivity analysis of the iPCoD DEB on the international KEC 5.0 scenario showed that the duration of disturbance per event has the largest influence on predicted population effects of any parameter tested, exceeding the effects of either density dependence or environmental stochasticity. Replacing the default 6-hour assumption with disturbance durations drawn from an Erlang distribution with a mean of 2 hours — a value more consistent with recent empirical observations — reduced predicted worst-case impacts to less than 1%. Density dependence and environmental stochasticity each reduce predicted impacts in their own right, and although they act through distinct mechanisms (compensatory per-capita resource increase under density dependence; larger energetic reserves and individual heterogeneity under environmental stochasticity), their effects are not additive: once animals have sufficient buffer (energy reserve) from one mechanism, the marginal protective effect of the other is reduced.

Analysis of alternative piling schedules showed that worst-case (5th percentile) population outcomes are highly sensitive to the temporal distribution of disturbance, while median (50th percentile) outcomes remain consistently small (<2%) across all scenarios tested. A "smoothed" version of the KEC 5.0 schedule, which distributed the same total disturbance more evenly across years and removed the pronounced peak in harbour porpoise disturbance days in 2027, reduced the worst-case decline from 23–25% to 8%, despite involving a slightly higher total number of piling days. Scenarios designed to avoid piling in August or September did not produce the expected reduction in impact: because the total piling effort was held constant, avoiding these months required redistributing disturbance into the remaining months and across more simultaneously active projects, which generated new annual peaks in disturbance. A positive effect of avoiding construction activities during these months may therefore be masked.

The consequences of these findings for regulatory interpretation are presented in the Recommendations section. Rather than prescribing a single "correct" model configuration, the recommendations describe the implications of particular choices around assessment metrics, model realism and disturbance duration. In summary:

- The 5th percentile of model output is shaped at least as much by parameter uncertainty (in particular the joint distribution of metabolic rate and resource availability calibrated by Approximate Bayesian Computation (ABC)) as by ecological worst-case conditions, and would be expected to move closer to the median as empirical knowledge of harbour porpoise energetics improves;
- The standard six-year post-disturbance window was defensible for iPCoD EE, where the population stabilises after disturbance, but in iPCoD DEB — where the population recovers — its value depends on where in the recovery trajectory it falls, so reporting additional quantities (e.g. the maximum decline over the simulation) gives a fuller picture;
- Switching density dependence and environmental stochasticity off does not yield a more precautionary estimate of a real-world effect, but rather an estimate of what the effect would be in a world without these biological processes; all reported population effects should therefore be understood as conditional on this assumption rather than as intrinsic properties of the scenarios modelled.

A roadmap for further model testing and development is also provided, covering re-parameterisation of the DEB component as new empirical data become available (notably from the Ecowende project), an empirical update of the disturbance-duration parameter, and dedicated analysis of seasonal sensitivity.

Finally, Appendix C lists the model parameters that were put forward as candidate topics for the November 2025 expert workshop on harbour porpoise condition in relation to offshore wind energy, and summarises for each how (and whether) it was addressed at the workshop, the main conclusions reached, and where the associated follow-up actions were placed on the short-, medium- and long-term research timelines.

2 Introduction

2.1 Introduction to iPCoD EE and iPCoD DEB

The interim Population Consequences of Disturbance (iPCoD) software developed by the University of St Andrews in 2013 allows users to evaluate the potential effects of disturbance events (such as the construction of offshore wind farms) on the population dynamics of five marine mammal species: harbour porpoise (HP), bottlenose dolphin, common minke whale, grey seal, and harbour seal (Harwood et al. 2014). In this iPCoD, the predicted effects of disturbance on individual vital rates (survival and fecundity) are calculated using transfer functions derived through structured expert elicitation (Booth et al. 2019), in which scientists were asked to estimate how many days of disturbance an animal can tolerate before its vital rates are affected, and by how much. Due to the variability in expert opinion, these functions result in large variability in model outputs between simulations (Harwood et al. 2013, Harwood et al. 2014a, Harwood et al. 2014b, Harwood and King 2017). Throughout this report, the original version of iPCoD is referred to as iPCoD EE, reflecting its reliance on expert elicitation to parameterise the key relationships in the model.

The dynamic bioenergetics model (DEB) developed by Harwood et al. (2020b) is based on a "cradle to grave" bioenergetics model originally developed for long-finned pilot whales by Hin et al. (2019). This model simulates the energy acquisition and expenditure of individual females over their lifetimes, including the effects of disturbance that results in reduced feeding. Rather than relying on expert opinion to define the relationship between disturbance and vital rates, the DEB model derives these relationships mechanistically from individual energy budgets, replacing the expert elicitation outputs in iPCoD EE to create iPCoD DEB (Harwood et al. (2024). iPCoD DEB is currently available for harbour porpoise only.

There are the following main differences and similarities in model structure and assumptions between iPCoD EE and iPCoD DEB:

1. **Transfer functions.** Both iPCoD EE and iPCoD DEB assume that all effects of disturbance on individuals occur via the energetic pathway — i.e. that individuals affected by a stressor stop foraging and their energy intake is reduced accordingly. Neither model considers potential effects of disturbance via non-energetic pathways (e.g., mother-calf separation, chronic stress). This assumption is built into iPCoD EE through the 2018 expert elicitation (Booth et al. 2019), in which experts defined a day of disturbance as a period of no energy intake lasting approximately 6 hours. The difference between the two models lies not in this underlying assumption, but in how the effect of lost feeding opportunities on vital rates is calculated: iPCoD EE uses expert-elicited transfer functions that relate cumulative days of disturbance directly to annual vital rates, whereas iPCoD DEB mechanistically tracks the energetic consequences of missed foraging at a daily time-step through the dynamic bioenergetic model.



2. **Resources:** iPCoD DEB explicitly models the prey resources available to individual animals, using a parameter R_{sim} that represents the per-individual resource density on a given day. R_{sim} is built each year from a baseline scalar, R_{mean} , which is sampled once per bootstrap iteration from an Approximate Bayesian Computation (ABC) posterior distribution and remains fixed for the whole simulation within that bootstrap. This is a structural difference from iPCoD EE, which has no explicit representation of resources: in iPCoD EE, environmental conditions enter the model only indirectly, through year-to-year variation in vital rates (see point 4). In iPCoD DEB, daily energy intake for each individual is derived from R_{sim} together with the animal's age, body size, body condition and reproductive state, and it is R_{sim} that links environmental conditions to individual energetics and, through them, to population-level outcomes. How R_{sim} is derived from R_{mean} depends on which model features are switched on:

- In the baseline configuration (no density dependence, no environmental stochasticity), R_{sim} is filled with a single constant value equal to R_{mean} . For a given iteration, it does not vary between days, between individuals, between years, or with season.
- When density dependence is switched on (see point 5), R_{mean} itself remains fixed for the iteration, but at the start of each year it is rescaled as a function of the current population size to give a year-specific baseline ($R_{mean_this_year}$). All else equal, a smaller population implies a higher $R_{mean_this_year}$ and therefore more food per head; the rescaling is bounded so that $R_{mean_this_year}$ cannot fall below R_{mean} , meaning density dependence acts only in the compensatory direction. Within a year, R_{sim} is still constant across days and individuals.
- When environmental stochasticity is switched on (see point 4), R_{sim} is filled with independent draws from a beta distribution centred on $R_{mean_this_year}$ (or on R_{mean} , if density dependence is off), with one independent draw per day and per individual. This means that R_{sim} fluctuates from day to day and between individuals on the same day, but the underlying R_{mean} (and $R_{mean_this_year}$) are unchanged.

Importantly, although disturbance reduces the energy intake of disturbed individuals on a given day (by the fraction of the day for which they cannot forage), it does not trigger any redistribution of resources to the rest of the population: resources that disturbed animals would otherwise have consumed are not reallocated to non-disturbed individuals, and neither R_{mean} nor $R_{mean_this_year}$ is adjusted as a result of disturbance. The environmental resource pool is therefore best thought of as describing per-individual availability, not a finite shared pool that depletes with consumption.

3. **Seasonal variation in disturbance effects.** The DEB component of the model tracks seasonal changes in individual body condition, reflecting dynamic variation in energy requirements driven by resource availability (see point 2) and energetic requirements. Consequently, the effect of disturbance may vary



across the year and be greatest during periods of higher energetic demand, such as lactation. In iPCoD EE, the effect of disturbance is constant throughout the annual cycle — users can specify different numbers of affected individuals across seasons, but the per-animal effect of disturbance remains fixed, based on the assumption that disturbed animals cease foraging for six hours.

4. **Environmental stochasticity.** In iPCoD EE, environmental stochasticity is implemented as year-to-year variation applied directly to vital rates: survival and fecundity rates are drawn each year from a beta distribution centred on their baseline values, with standard deviations set through expert elicitation (Harwood et al. 2014). This variation is imposed directly on the demographic rates themselves, independently of any biological mechanism. In iPCoD DEB, there are no directly imposed year-to-year fluctuations in vital rates. Instead, environmental stochasticity enters the model through daily variation in resource availability: each simulated individual's energy intake fluctuates around a mean resource density, which causes variation in individual body condition over time. Changes in body condition then propagate through the bioenergetics model to affect vital rates — reproduction and survival — as emergent outcomes. Environmental stochasticity in iPCoD DEB therefore reflects a biologically explicit pathway from resource variability to individual condition to population-level demographic outcomes, rather than a direct statistical perturbation of vital rates. In the absence of disturbance, including or excluding environmental stochasticity results in similar overall population trajectories, as parameter combinations are calibrated to reproduce comparable population growth rates and demographic patterns. However, the underlying parameterisation differs between these cases, particularly in the value of mean resource density (R_{mean} , see point 2), which must shift to compensate for fluctuations of resource variability in order to meet the same population-level constraints.
5. **Density dependence.** In iPCoD EE, density dependence operates through a single, direct pathway: fecundity (birth rate) is adjusted as a function of current population size using a generalised logistic equation (Taylor and DeMaster 1993), with parameters for maximum fecundity, fecundity at carrying capacity, and the shape of the relationship. This means that as population size declines below carrying capacity, birth rates increase, but all other vital rates remain unaffected by density. In iPCoD DEB, density dependence is an emergent property of the bioenergetics model and operates through a mechanistic chain: as the population declines, there is more prey available per individual; increased prey availability improves individual energy intake; improved energy intake leads to better body condition; and improved body condition results in higher birth rates and improved calf survival. Unlike iPCoD EE, where only fecundity responds to population size, iPCoD DEB allows multiple vital rates to respond to density, through the shared pathway of individual body condition. The quantitative relationship between resource availability and population size used to implement density dependence in iPCoD DEB was derived from a multi-generational bioenergetic population model developed by Vincent Hin (Wageningen Marine Research), in which prey dynamics and porpoise population dynamics are modelled jointly to estimate equilibrium (carrying capacity) conditions and the functional relationship between prey density

and abundance (see Section 6 in Harwood et al. (2024)). In both models, density dependence allows the population to recover following disturbance-driven declines, but the speed and nature of that recovery differ between the two approaches.

6. **Definition and specification of the disturbance effect.** In iPCoD EE, the per-animal effect of a disturbance event was fixed during the expert elicitation process: experts were asked to assume that each disturbance event results in a six-hour cessation of foraging, equivalent to a 25% reduction in daily energy intake. This value is built into the transfer functions and cannot be changed by the user. In iPCoD DEB, the duration of foraging lost per disturbance event — referred to as the "effect of disturbance" — is a user-specified parameter. By default, it is also set to 6h.
7. **Modelled species.** iPCoD EE can be used to model the effect of disturbance on five marine mammal species: harbour porpoise, bottlenose dolphin, common minke whale, grey seal, and harbour seal. Currently, the iPCoD DEB model exists only for harbour porpoises. Although the DEB components are developed for all the remaining four species, they have not been incorporated (yet) into iPCoD DEB (Harwood et al. 2014, Harwood et al. 2024).

All remaining processes, such as initial population age structure and the probability of each individual being disturbed, are modelled identically in iPCoD DEB and iPCoD EE. In particular, iPCoD DEB v2.0 (the model version as a result of this project) now runs with true matched pairs of impacted and unimpacted populations — as iPCoD EE does — meaning that within each matched pair both populations are initialised with the same age structure, receive the same sequence of stochastic draws for demographic and environmental processes, and use the same sampled parameter values, with the only difference being whether disturbance impacts are allocated to individuals. As a consequence, when the modelled stressor has a negligible effect on vital rates, the impacted and unimpacted populations within a matched pair produce exactly the same outputs, and the counterfactual metrics used for presenting iPCoD EE results (e.g. the difference between impacted and unimpacted population size at the end of the simulation, percentile-based impact estimates) can now be applied to iPCoD DEB in exactly the same way.

As reported in the KEC 5.0 assessment (Heinis et al. 2025), the iPCoD DEB model (version 1.0) produced a markedly lower estimated effect of disturbance than iPCoD EE for the same disturbance scenarios. For the international KEC 5.0 scenario (2016–2031) applied to the North Sea harbour porpoise population, iPCoD DEB yielded a more stable population trajectory with a narrower spread of outcomes and — unlike iPCoD EE — did not predict a significant reduction in population size as a result of disturbance; the spread that iPCoD DEB did produce was approximately symmetric around zero and attributable to stochastic variation in the simulation rather than to a systematic effect of disturbance. This divergence raised concerns from regulators, and as a precautionary measure the KEC 5.0 assessment retained the iPCoD EE results for comparison against the Dutch ecological standard, with SMRUC advising that the outputs of both models be considered together when assessing population-level effects. The divergence also highlighted the need for additional simulations and

targeted model testing. The structural differences listed above (points 1-6) were identified as the likely main reasons why the outcomes of the two models differ for the same disturbance scenario; however, it was not yet understood when and how each of these factors affected simulation outcomes.

The DEB part of the iPCoD DEB model requires values for more than 50 parameters, some of which are not directly observable. The Ecowende, Utrecht University, RWS-Wozep project, which aims to advance understanding of body condition effects on reproduction and health of harbour porpoises in the southern North Sea, is expected to provide valuable empirical constraints on a number of these parameters, including the reproductive cycle of females (conception, lactation period, gestation length, and calving season) and links between body condition and reproductive performance. The Ecowende project is expected to run from 2025 to 2029. It held a workshop in autumn 2025 which brought together experts in the field from different disciplines to discuss how the Ecowende project can contribute to a more robust DEB parameterisation, and how improved understanding of the most influential DEB parameters can help shape future research priorities within the Ecowende project.

2.2 Use of iPCoD models (EE and DEB) in KEC 5.0

In the KEC 5.0 framework (Heinis et al. 2025), outputs from iPCoD models are used to quantify population-level effects of cumulative disturbance by underwater sound from offshore wind farm installation (expressed as animal disturbance days) on marine mammals. Model results are typically summarised as the difference between disturbed and undisturbed population trajectories. For regulatory assessment, the predicted population decline is compared against the ecological standard that population reduction due to the considered disturbance must not exceed 5%, with high confidence (>95%). Assuming that population effects of disturbance stabilise after disturbance ends, the decline is calculated over a period following the cessation of disturbance. In previous KEC reports, the population reduction calculated by iPCoD EE was averaged over a period of six years after the final year of piling.

To achieve 95% confidence in the predicted population reduction, the KEC assessment framework relied on the statistics of the expert opinions in iPCoD EE, by calculating the 5th percentile of the population reductions calculated in many model runs (e.g. 20.000 runs in KEC 5.0).

This statistic is then used to determine whether the modelled scenario complies with the ecological threshold or requires mitigation.

The iPCoD DEB model did not predict a significant reduction in the harbour porpoise population in the KEC 5.0 study. Because there was then very little experience with the new model, the comparison with the ecological standard was made for the reduction calculated with the iPCoD EE model, in a cautious approach.

2.3 Goals of the assignment

The main objectives of this assignment were:

- a) To conduct a range of simulations that clarify when and why the two versions of the iPCoD model — iPCoD EE and iPCoD DEB produce different, or similar, estimates of stressor effects on harbour porpoise populations for the same disturbance scenarios. This work had a specific focus on the assessment metric currently used in the Netherlands (a 5% population decline threshold applied with 95% confidence, rather than a comparison of medians between the two models) and aimed to deliver an explanatory output that regulators can draw on when deciding which model to use in assessments.
- b) To understand the sensitivity of the results of iPCoD DEB when density dependence and environmental stochasticity components are used.
- c) To assess which parameters of the DEB component, and of iPCoD DEB more broadly, could be updated with new empirical information, and to identify how the Ecowende project could be tailored to deliver the data required for such updates (work package 3, WP3).
- d) To produce a roadmap for further sensitivity analysis of iPCoD DEB, identifying the parameters and processes that most warrant additional investigation, the scenarios against which they should be tested, and the order in which this work should be prioritised.
- e) To provide a set of practical recommendations, grounded in the outputs of this assignment, describing the advantages and limitations of iPCoD EE and iPCoD DEB and the circumstances under which each model is most appropriate. These recommendations are intended to support regulators, assessors and developers in deciding which model — or combination of models — is best suited to a given assessment.
- f) To translate the findings of this work into specific recommendations for the next iteration of the KEC 6.0, including how iPCoD DEB outputs could be used alongside or in place of iPCoD EE outputs in cumulative effects assessments of offshore wind farm construction in Dutch and North Sea waters.

The preliminary results of addressing point a) showed that iPCoD DEB v1.0 used in KEC 5.0 had a major bug which was the main reason between the discrepancies between iPCoD EE and iPCoD DEB in how these models predict the effect of offshore constructions tested in KEC 5.0. Additionally, iPCoD DEB v1.0 model required powerful computers to run, and each simulation lasted at least two hours. This was a limiting factor for the number of simulations that could be conducted. As part of this assignment, we, therefore, included an extensive description of model debugging and improvement of code performance. These results are presented in the Appendix A, and only short summaries are included in the main text.

3 Methods

3.1 General approach

This project combined code development, model debugging, and simulation analyses to address the goals of the assignment. Rather than presenting methods separately from results, detailed methodological descriptions are

provided alongside corresponding results in Section 4, as the rationale for specific analytical choices is best understood in context. This section provides an overview of the general simulation framework and piling scenarios used throughout the analyses.

All simulations of iPCoD EE in this study were performed using iPCoD 5.2¹ using model parameters as in KEC 5.0 for low fecundity HP population (see Table 4.2 in Heinis et al. (2025)). All simulations of iPCoD DEB in KEC 5.0 were done using iPCoD DEB v 1.0 and in this study using iPCoD DEB v2.0.

3.2 Simulation framework

All simulations were performed using the iPCoD DEB v2.0 model coded in R (version 4.0.0, R-Core-Team (2023)). Unless otherwise stated, simulations were run with 300 bootstrap iterations ($n_{boot} = 300$) to ensure adequate characterisation of parameter uncertainty. The simulations were run for 28 years: 1 year of initial population run in the absence of disturbance, 21 years with piling (see section 3.3) and 6 years post-piling. Each iteration samples a unique combination of DEB parameters from an Approximate Bayesian Computation (ABC) posterior distribution (Chudzińska et al. 2024, Harwood et al. 2024), which was calibrated to produce realistic population growth rates and birth rates for harbour porpoises in the absence of disturbance. The simulated population consisted of 1,500 females ($sim_number = 1,500$), scaled to represent the North Sea harbour porpoise population ($p_{mean} = 373,310$ individuals) (Gilles et al. 2020).

Unless otherwise stated, to investigate the effects of model configuration on simulation outcomes, analyses were conducted under four configurations representing all combinations of:

- Density dependence: included (DD) or excluded (no DD)
- Environmental stochasticity: included or excluded

When environmental stochasticity was included, daily resource availability for each individual was drawn from a beta distribution, introducing both temporal and individual variation in foraging success. In the absence of the environmental stochasticity, for a given day, daily resources available was the same for all individuals. When density dependence was included, per-capita resource availability increased as population size declined below carrying capacity, allowing for compensatory population recovery.

3.3 Piling scenarios

All simulations involving disturbance were based on the international piling schedule presented in KEC 5.0 (Heinis et al. 2025), which represents a cumulative scenario of offshore wind farm construction across the North

¹ KEC 5.0 uses iPCoD EE 6.0 for the simulations. This version differs from iPCoD EE 5.2 by having extra functionality added which is not used in the modelling process. Hence, results of simulations of versions 5.2 and 6.0 should be similar.

Sea in years 2016-2031. On the basis of the data provided, TNO developed an algorithm for creating a generic calendar for this scenario (see section 5.1 in Heinis et al. (2025)) using the following steps:

Step 1: scenario supplied by RWS states the year of construction for each wind farm (project).

Step 2: a calendar of piling days was generated using that scenario with the following assumptions:

- Since detailed information about the piling days was not available for KEC 5.0, an arbitrary starting date is selected for each project in the planned year for the construction.
- Because the maximum number of projects that can be executed simultaneously is limited by the number of available piling vessels, it is assumed that a maximum of seven piling projects can be executed simultaneously (two Dutch projects plus five projects in the other North Sea countries).
- In all cases, it is assumed that for each project three piles are driven on consecutive days, after which there are three days without piling to bring in new piles.

The schedule spans 21 years (2011-2031) with piling activity for 132 individual piling projects in the years 2016-2031. This means that there is no disturbance in the first 6 years (so called 'burn-in' period, including the first year of initial population run). Unless otherwise specified, disturbed animals were assumed to lose 6 hours of foraging time per disturbance day, consistent with assumptions used in previous KEC assessments. The number of disturbed animals per day at each operation was also as calculated in KEC 5.0.

To investigate the sensitivity of model predictions to the timing of disturbance, modified piling schedules were developed. The original scenario considered the starting year for each project, meaning that, even if piling vessels are available, a new project wouldn't start before the planned year. Figure 3-1 shows the annual numbers of piling days and porpoise disturbance days for this scenario.

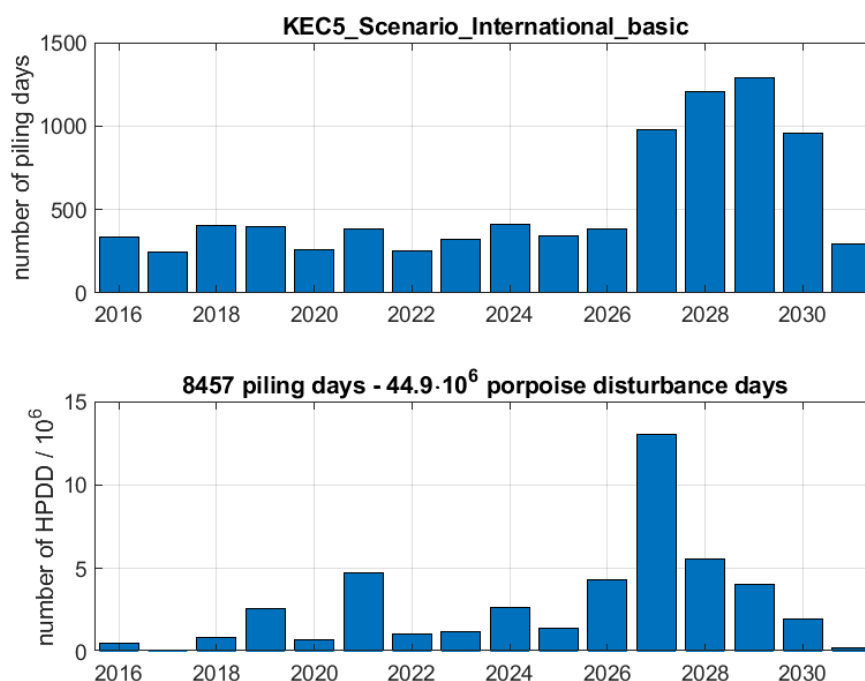


Figure 3-1. Number of piling days per year (upper graph) and number of harbour porpoise disturbance days (HPDD) per year (lower graph) in the basic KEC 5.0 scenario, over the period 2016-2031.

The KEC 5.0 scenario has a strong peak in harbour porpoise disturbance days in 2027. This is mainly caused by planned large wind farm construction projects without noise mitigation.

To investigate the consequence of the large annual variation of piling days on the population trends, a ‘smoothed’ variant of the original scenario was created which does not consider the starting years and starts a new project as soon as another is finished. The same piling projects (with the same number of disturbed animals per piling day and the same 3 days on / 3 days off of piling per project) are kept but are more uniformly distributed over the years. To spread the total duration of all projects over a period similar to the original, it was assumed that a maximum of four piling project can be executed simultaneously in this scenario (one Dutch project plus three projects in the other North Sea countries). The total number of piling days is 6% higher than in the original scenario, in which the algorithm delayed some piling days till after 2031, outside the calculation window (Figure 3-2).

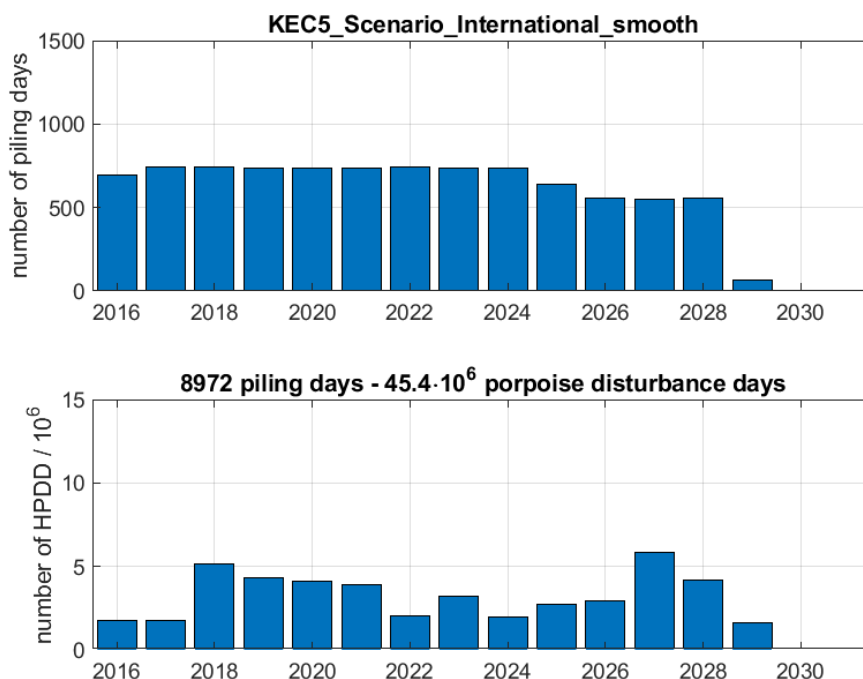


Figure 3-2. Number of piling days per year (upper graph) and number of harbour porpoise disturbance days (HPDD) per year (lower graph) in the 'smoothed' KEC 5.0 scenario.

In addition, two other variants of the original KEC 5.0 scenario were created in which piling projects avoided the months of August or September. These months have been shown to have critical importance in porpoise lactation and preparation for the winter (Harwood et al. 2020a, Gallagher et al. 2021). The algorithm for building piling schedule was applied with the constraint to avoid one of both months. To compensate for the delay, it was assumed for these scenarios that nine projects were allowed to pile at the same time (three Dutch projects and six projects in the other North Sea countries). The total number of piling days remained unchanged for all scenarios.

3.4 Sensitivity of the model predictions to presence of density dependence mechanism, environmental stochasticity and duration of disturbance

To understand the relative importance of key iPCoD DEB v2.0 model parameters on predicted population effects, a series of simulations was conducted using the international KEC 5.0 piling scenario. Three parameters were systematically varied:

- **Density dependence (DD):** included or excluded (see point 5 in Section 2.1 for assumptions)
- **Environmental stochasticity:** included or excluded (see point 4 in Section 2.1 for assumptions)
- **Duration of disturbance:** fixed at 6 hours, drawn from an Erlang distribution with mean = 6 hours (Erlang 6), or drawn from an Erlang distribution with mean = 2 hours (Erlang 2)

The Erlang distribution introduces variation in disturbance duration among individuals within a simulation, in contrast to the fixed duration assumption where all disturbed animals lose exactly 6 hours of foraging time. (Figure 3-3).

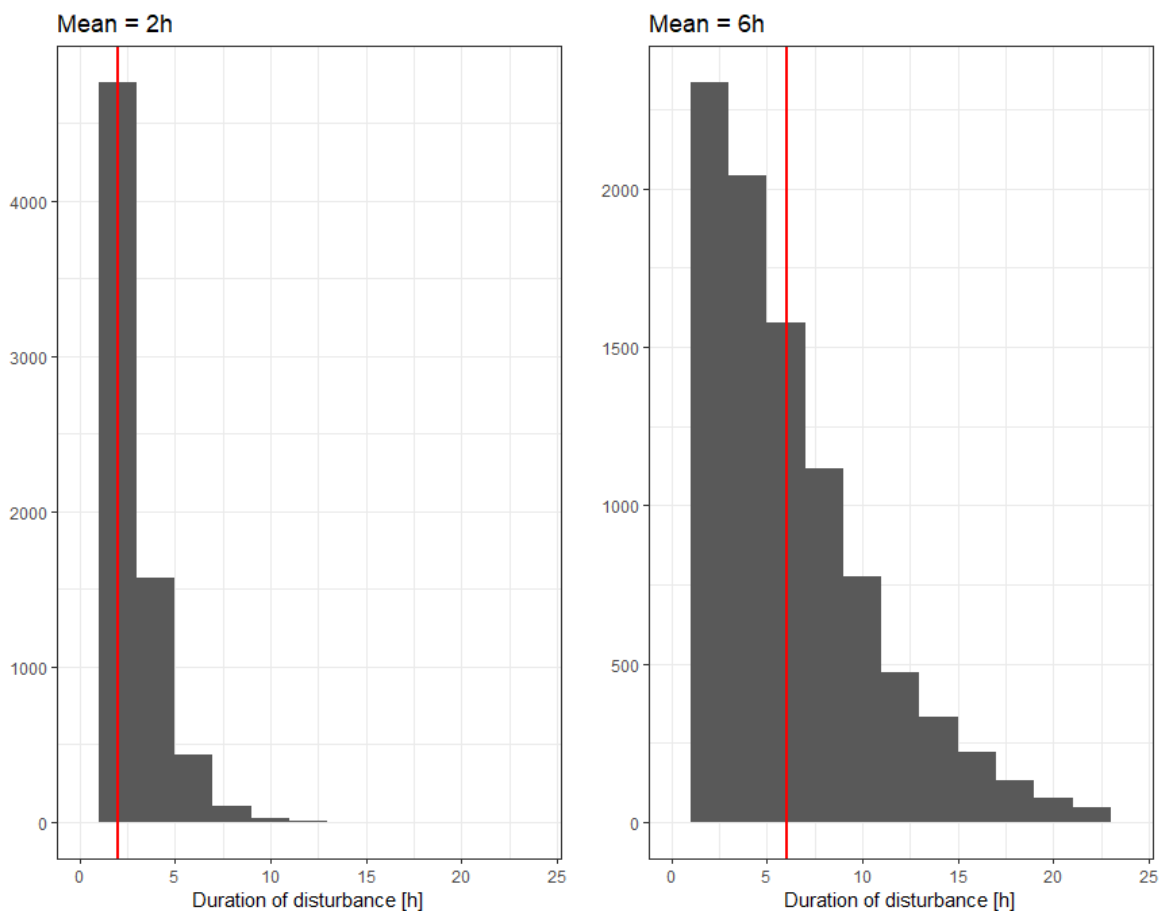


Figure 3-3. Distribution of duration of disturbance (h) drawn from an Erlang distribution with means equals to 2 and 6. The Y axis show number of draws from a total of 10,000.

The two distributions of duration of disturbance are based on different mean values but have the same shape parameter (shape parameter of the distribution, $k=3$). Using mean = 6h was used for comparison with iPCoD EE and the current default value in iPCoD DEB v2.0 based on the duration of disturbance assumed in the expert elicitation that underpins iPCoD EE v5.2, where experts were asked to assume that each disturbance event resulted in a 6-hour cessation of foraging (Harwood and King 2014, Booth et al. 2019). However, rather than applying a fixed 6-hour value uniformly to all disturbed individuals, an Erlang distribution was used to capture the expected heterogeneity in individual responses. In reality, the effect of disturbance on any given animal depends on its location relative to the noise source at the onset of piling. Animals located closer to the source experience higher received sound levels, are likely to be displaced over greater distances, and consequently lose more foraging time before they can resume normal behaviour. Conversely, animals situated further from the source, towards the periphery of the disturbance zone, experience lower received levels and shorter

displacement distances, resulting in shorter periods of foraging disruption. Given that, for a uniform distribution of animals, the number of individuals increases with distance from the source (proportional to the area of concentric rings). Therefore, the majority of disturbed animals will be located in the outer regions of the impact zone and will experience relatively short disturbance durations. The Erlang distribution captures this pattern: the distribution is right-skewed, with a mode below the mean, such that most individuals experience disturbance durations shorter than 6 hours, while a smaller proportion of animals closer to the source occupy the upper tail of the distribution and experience longer disruptions. This approach provides a more biologically realistic representation of population-level responses to piling than applying a single fixed value to all individuals.

The distribution of disturbance based on mean = 2h was derived from an extensive literature review and data analysis of the effect of disturbance on harbour porpoise. This review integrated observed swimming speeds of harbour porpoise with dose-response relationships from Graham et al. (2019) to estimate the time required for disturbed animals to exit the affected area (see details, including references, in Appendix 1 of Harwood et al. (2024)).

3.5 Output metrics

Following alignment of iPCoD DEB with the iPCoD EE framework, population-level effects of disturbance were quantified as the difference in population size between matched pairs of impacted and unimpacted populations. Results are presented as the 5th, 50th, and 95th percentiles of this metric across the 300 bootstrap iterations, calculated over the six years following the end of all piling operations, consistent with KEC 5.0 (Heinis et al, 2025). When applicable, we also present other metrics like maximum population decline over the simulation time, or total population size.

4 Results

4.1 Model debugging, diagnostics and improving code performance

Substantial improvements were made to the iPCoD DEB model to enhance computational efficiency and ensure robust simulation outcomes. Code optimisation, primarily through vectorisation of the daily simulation loop and removal of redundant calculations, reduced runtime by approximately 5–10 times. Additional gains were achieved by restructuring simulations to use matched pairs of disturbed and undisturbed populations, improving both efficiency and comparability with the iPCoD EE framework.

In parallel, extensive debugging identified and resolved several critical issues affecting model behaviour. The most significant bug involved incorrect processing of the piling schedule, which previously resulted in only a small fraction of disturbance events being applied. Other major fixes addressed inconsistencies in stochastic processes, incorrect handling of orphaned calves, and mismatches between disturbed and undisturbed

simulations. Collectively, these corrections ensure that model outputs now accurately reflect disturbance effects, with differences between scenarios attributable solely to the intended model mechanisms rather than coding errors. iPCoD DEB v2.0 is the results of this debugging and code performance improvements.

Model diagnostics further showed that the most extreme population declines under disturbance are driven by specific combinations of biological parameters. In particular, simulations with high basal metabolic rates and low resource availability produced individuals with limited energetic reserves, making them less able to buffer periods of reduced foraging during disturbance. Under these conditions, disturbance leads to higher mortality in energetically demanding life stages, especially among pregnant and lactating females, which in turn amplifies population-level declines. These extreme outcomes occur in a relatively small subset of simulations but strongly influence worst-case (5th percentile) results.

The analyses also showed that, in the iPCoD DEB model, populations can recover after disturbance even in the absence of density dependence. This recovery arises from disturbance-induced shifts in population structure: energetically stressed reproductive females are disproportionately affected, while younger, non-reproductive individuals are less impacted. As disturbance ceases, these surviving immature individuals mature and enter the breeding population, leading to a rebound in reproduction and subsequent population recovery. Including environmental stochasticity in the model substantially reduces the predicted magnitude of disturbance effects. By introducing variability in resource availability and individual energy intake, environmental stochasticity increases heterogeneity in individual responses and reduces the likelihood that large fractions of the population simultaneously experience severe energetic stress. As a result, both worst-case (5th percentile) and median population declines are dampened compared to simulations without environmental stochasticity.

Further details on the optimisation process and debugging steps are provided in the Appendix A. This includes a breakdown of which model parameters most strongly influence computational time, a full list of identified bugs and their severity, and additional diagnostic analyses used to verify correct model behaviour.

4.2 Comparison between model predictions of iPCoD EE and iPCoD DEB

The comparison between iPCoD EE and iPCoD DEB v2.0 simulations revealed notable differences in the predicted population trajectories under disturbance (Figure 4-1, Table 4-1). The trajectories show the steepest decline in the years after the peak in porpoise disturbance days in 2027 so years 19-21 of the simulations (see also Figure 3-1). In iPCoD EE (Figure 4-1 top left), the population decline at the 5th quantile began earlier in the simulation period and showed almost no recovery after disturbance ceased, with the mean 5th quantile remaining at -17% difference between undisturbed and disturbed population during the six years post-disturbance compared to a maximum of -19% during the disturbance period. In contrast, iPCoD DEB simulations demonstrated clear population recovery following the cessation of disturbance, even in the absence of density-dependent compensation (see section 4.1 and Appendix A to understand why).

Without environmental stochasticity and without density dependence (therefore using the settings closest to iPCoD EE settings), iPCoD DEB (Figure 4-1 top middle) produced a slightly higher maximum decline at the 5th quantile (–22%) than iPCoD EE (–19%), but the population subsequently recovered to –13% averaged over the post-disturbance period of 6 years after disturbance. Including density dependence further reduced the maximum decline over the entire simulation to –12% (Figure 4-1 top right). The inclusion of environmental stochasticity substantially reduced the predicted magnitude of disturbance effects across all quantiles (see section 4.1 and Appendix A to understand why this is the case) (Figure 4-1 bottom left and middle), with the combination of density dependence and environmental stochasticity yielding the smallest impacts (post-disturbance 5th quantile: –2%; maximum: –3%) (Figure 4-1 bottom left).

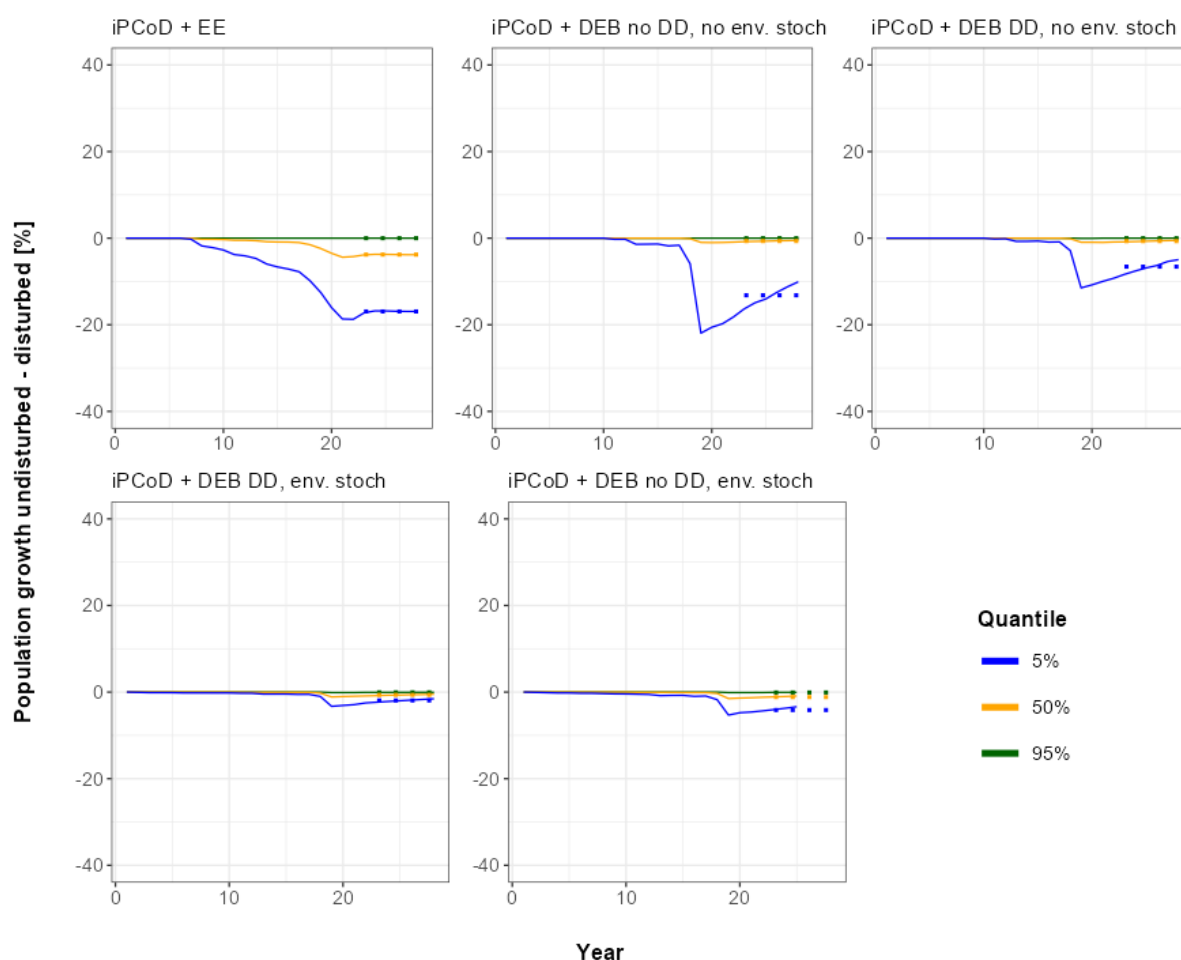


Figure 4-1. Comparison of the percent difference between disturbed and undisturbed harbour porpoise populations over a 28-year simulation period for iPCoD EE and four configurations of iPCoD DEB. Lines represent the 5th (blue), 50th (orange), and 95th (green) quantiles across simulations. Dashed lines show mean quantiles over the six years after disturbance ceased to align with approach used in KEC. iPCoD DEB model configurations vary by inclusion of density dependence (DD) and environmental stochasticity (env. stoch). Piling occurred between years 6 and 21 of the simulations. The last 7 years of simulations is a post-piling period. There is no density dependence and environmental stochasticity included in iPCoD EE.

Table 4-1. Summary statistics of the percent difference between disturbed and undisturbed populations for iPCoD EE and iPCoD DEB model configurations. Values show the mean of the 5th, 50th, and 95th quantiles during the six years following cessation of disturbance, and the maximum decline value of the 5th quantile (max 5th) observed over the simulations. DD = density dependence; env. stoch = environmental stochasticity.

Model	5th	50th	95th	max 5th
iPCoD EE	-16.9	-3.8	0	-18.7
iPCoD DEB no DD, no env, stoch	-13.2	-0.7	0	-21.9
iPCoD DEB DD, no env, stoch	-6.6	-0.7	0	-11.5
iPCoD DEB DD, env, stoch	-2.0	-0.7	-0.06	-3.3
iPCoD DEB no DD, env, stoch	-4.2	-1.2	-0.09	-5.3

4.3 Sensitivity of the model predictions to presence of density dependence mechanism, environmental stochasticity and duration of disturbance

To understand the relative importance of key iPCoD DEB v2.0 model parameters on predicted population effects, a series of simulations was conducted using the international KEC 5.0 piling scenario. Three parameters were systematically varied:

- **Density dependence (DD):** included or excluded
- **Environmental stochasticity:** included or excluded
- **Duration of disturbance:** fixed at 6 hours, drawn from an Erlang distribution with mean = 6 hours (Erlang 6), or drawn from an Erlang distribution with mean = 2 hours (Erlang 2), see Section 3.4 for explanation.

The two distributions of duration of disturbance are based on different mean values but have the same shape parameter (shape parameter of the distribution, $k=3$). Using mean = 6h was used for comparison with iPCoD EE and the current default value in iPCoD DEB v2.0 based on the duration of disturbance assumed in the expert elicitation that underpins iPCoD EE v5.2, where experts were asked to assume that each disturbance event resulted in a 6-hour cessation of foraging (Harwood and King 2014, Booth et al. 2019). However, rather than applying a fixed 6-hour value uniformly to all disturbed individuals, an Erlang distribution (shape parameter $k = 3$) was used to capture the expected heterogeneity in individual responses. In reality, the effect of disturbance on any given animal depends on its location relative to the noise source at the onset of piling. Animals located closer to the source experience higher received sound levels, are likely to be displaced over greater distances, and consequently lose more foraging time before they can resume normal behaviour. Conversely, animals situated further from the source, towards the periphery of the disturbance zone, experience lower received levels and shorter displacement distances, resulting in shorter periods of foraging disruption. Given that, for a uniform distribution of animals, the number of individuals increases with distance from the source (proportional to the area of concentric rings). Therefore, the majority of disturbed animals will be located in the outer regions

of the impact zone and will experience relatively short disturbance durations. The Erlang distribution captures this pattern: the distribution is right-skewed, with a mode below the mean, such that most individuals experience disturbance durations shorter than 6 hours, while a smaller proportion of animals closer to the source occupy the upper tail of the distribution and experience longer disruptions. This approach provides a more biologically realistic representation of population-level responses to piling than applying a single fixed value to all individuals.

The distribution of disturbance based on mean = 2h was derived from an extensive literature review and data analysis of the effect of disturbance on harbour porpoise. This review integrated observed swimming speeds of harbour porpoise with dose-response relationships from Graham et al. (2019) to estimate the time required for disturbed animals to exit the affected area (see details, including references, in Appendix 1 of Harwood et al. (2024)).

Results of the effects of density dependence (DD) and environmental stochasticity on the simulation results are shown in Figure 4-1. These are based on an assumed fixed 6h disturbance per disturbance day. Results of the simulations for other disturbance durations are shown in Figure 11-1 (Appendix B). Model outputs are summarised in Table 4-2 as the 5th, 50th, and 95th percentiles of population change between disturbed and undisturbed populations averaged over the six years after disturbance ceased.

Table 4-2. Simulation results showing population change relative to undisturbed scenario (%) at the 5th, 50th, and 95th percentiles for different model configurations. DD = density dependence; Env. stochasticity = variation in daily resource availability. 5th percentiles are standard use in KEC.

5th (%)	50th (%)	95th (%)	DD	Env. stochasticity	Disturbance
-13	-0.7	0	No	No	Fixed 6h
-17.0	-1.8	-0.1	No	No	Erlang 6h
-0.2	0	0	No	No	Erlang 2h
-3.1	-0.8	-0.0	No	Yes	Fixed 6h
-5.7	-1.7	-0.2	No	Yes	Erlang 6h
-0.8	-0.1	0	No	Yes	Erlang 2h
-6.6	-0.7	0	Yes	No	Fixed 6h
-6.4	-1.4	-0.1	Yes	No	Erlang 6h
-0.2	0	0	Yes	No	Erlang 2h
-1.9	-0.7	-0.1	Yes	Yes	Fixed 6h
-5.7	-1.3	-0.1	Yes	Yes	Erlang 6h



-0.4	-0.1	0	Yes	Yes	Erlang 2h
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To assess relative parameter importance, standardised regression coefficients were calculated from linear models predicting each percentile from the considered parameters. Figure 4-2 to Figure 4-4 show the calculated coefficients for the three percentiles of the population reduction. The relative importance of parameters differed depending on which percentile was considered.

For the 5th percentile (worst-case scenarios), decreasing the disturbance duration (Erlang 6h to Erlang 2h) resulted in the largest reduction in population impact, followed by environmental stochasticity and density dependence. Without density dependence and environmental stochasticity, the worst-case population decline reached -13% with fixed 6-hour disturbance but was reduced to just -0.2% with Erlang 2h disturbance (Table 4-2). Including environmental stochasticity substantially reduced worst-case impacts (e.g., from -13% to -3% with fixed 6h disturbance and no DD). When disturbance duration was drawn from an Erlang distribution with mean = 6 hours, the predicted population impact increased compared to simulations assuming a fixed 6-hour effect, likely due to some individuals experiencing disturbance durations longer than 6 hours (Figure 4-2, Table 4-2).

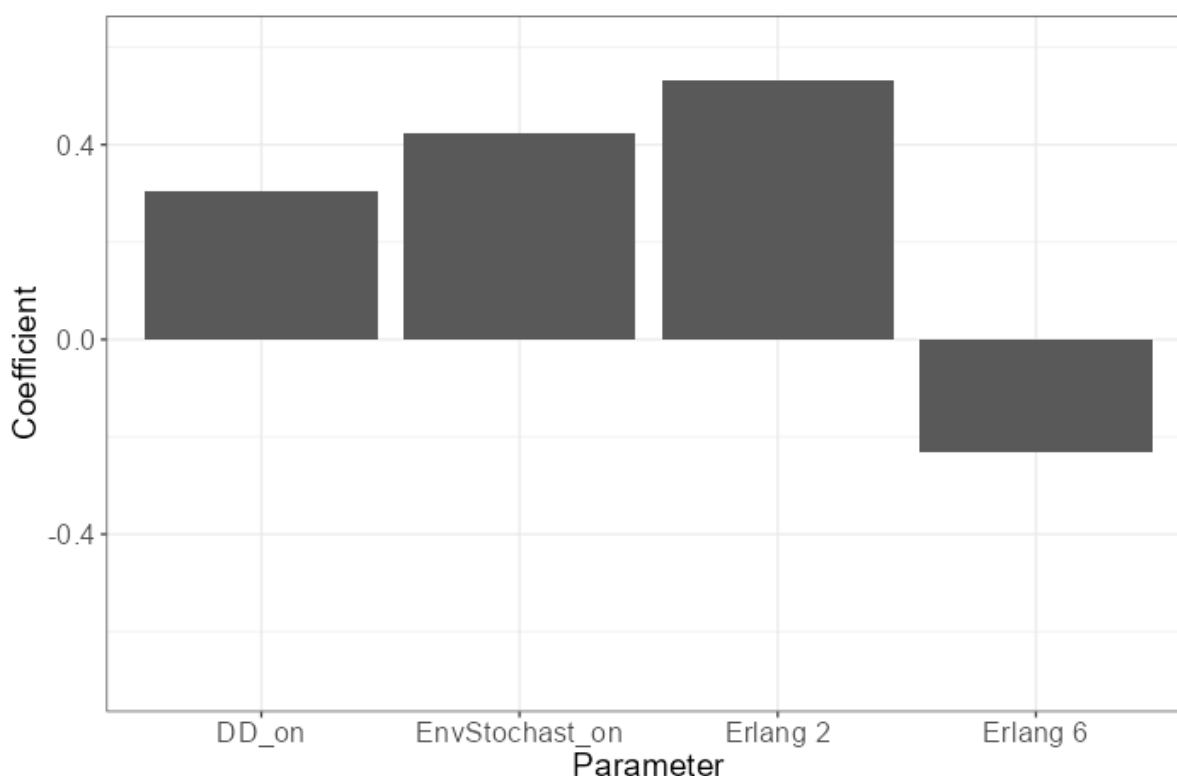


Figure 4-2. Standardised regression coefficients showing the relative importance of model parameters on the 5th percentile (worst-case) of population change. Positive coefficients indicate that the parameter reduces the negative impact of disturbance on the population. DD = density dependence; EnvStochast = environmental stochasticity; Erlang 2 and Erlang 6 = disturbance duration drawn from Erlang distributions with means of 2 and 6 hours, respectively.



For the 50th percentile (median scenarios), using disturbance duration drawn from the Erlang 6h distribution resulted in the largest negative effect on the population. As with worst-case scenarios (5th percentile), decreasing disturbance duration (Erlang 2h) produced the largest reduction in population impact, followed by density dependence and environmental stochasticity (Figure 4-3, Table 4-2).

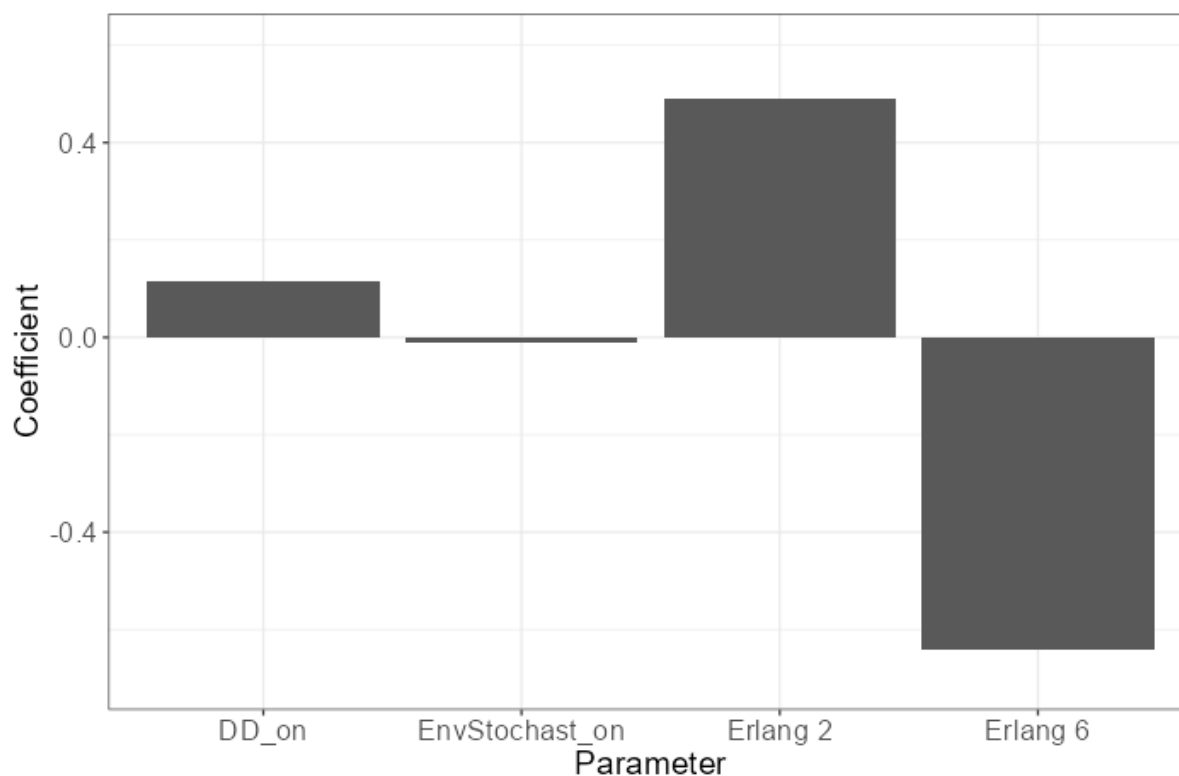


Figure 4-3: Standardised regression coefficients showing the relative importance of model parameters on the 50th percentile (median scenario) of population change. Positive coefficients indicate that the parameter reduces the negative impact of disturbance on the population. DD = density dependence; EnvStochast. = environmental stochasticity; Erlang 2 and Erlang 6 = disturbance duration drawn from Erlang distributions with means of 2 and 6 hours, respectively.

For the 95th percentile (best-case scenarios), increasing disturbance duration variability (Erlang 6h) had the largest negative effect. Including environmental stochasticity also had a slight negative effect on best-case outcomes, which can be explained by the increased spread of population trajectories when environmental variation is included (Figure 4-4, Table 4-2).

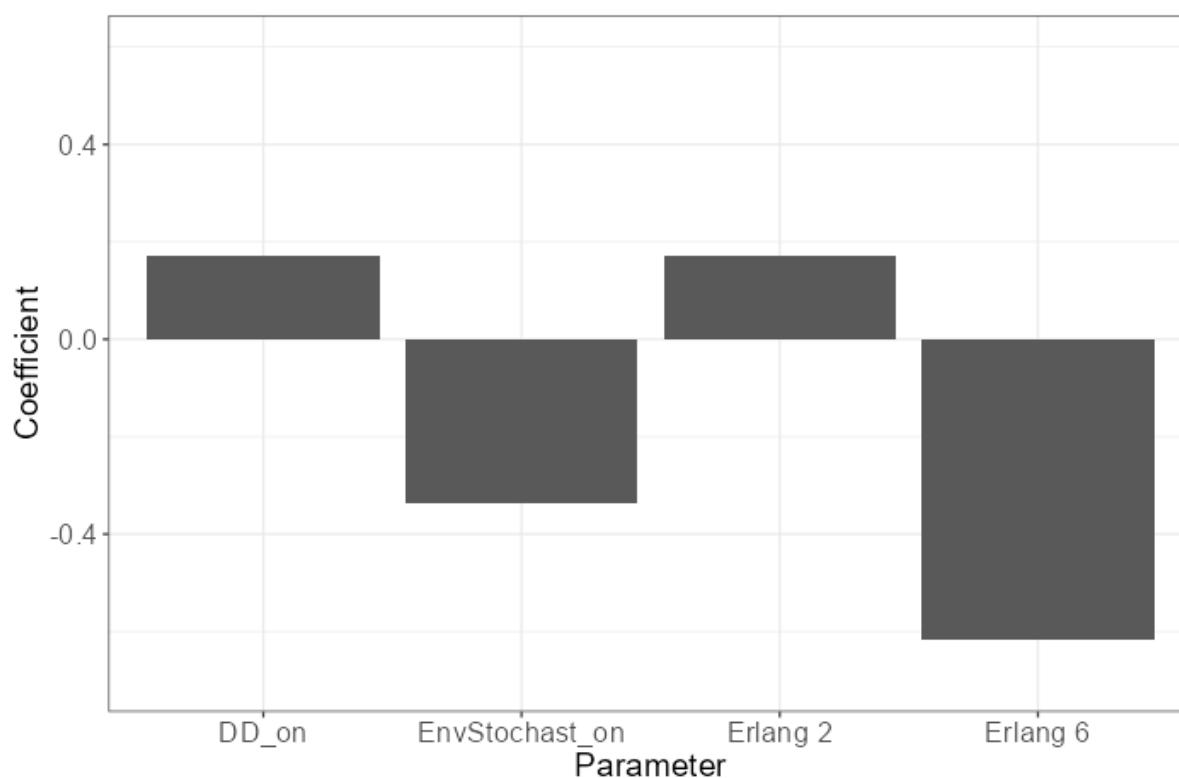


Figure 4-4. Standardised regression coefficients showing the relative importance of model parameters on the 95th percentile (best-case scenario) of population change. Positive coefficients indicate that the parameter reduces the negative impact of disturbance on the population. DD = density dependence; EnvStochast. = environmental stochasticity; Erlang 2 and Erlang 6 = disturbance duration drawn from Erlang distributions with means of 2 and 6 hours, respectively.

4.4 Understanding the effect of environmental stochasticity and density dependence on population dynamics

The inclusion of environmental stochasticity in the iPCoD DEB model affects both undisturbed population trajectories and the predicted impact of disturbance. Understanding these effects is important for interpreting model outputs and comparing results across different model configurations.

When environmental stochasticity is included in the simulations, the spread of population trajectories (i.e., the range between the 5th and 95th percentiles) is substantially larger than when it is excluded, and this applies to both when DD is included or not (Figure 10-1 in Appendix A). This increased variability arises because environmental stochasticity introduces an additional source of randomness between iterations. Without environmental stochasticity, variation between iterations stems solely from demographic stochasticity (random variation in survival and reproduction). With environmental stochasticity, different iterations experience different "luck" with resource availability—some iterations may have consistently favourable foraging conditions while others do not.

Counterintuitively, including environmental stochasticity reduces the predicted impact of disturbance on the population, particularly for worst-case (5th percentile) scenarios (Table 4-2). This effect can be explained by differences in the mean resource availability (R_{mean}) parameter between the two configurations.

The inclusion of both density dependence and environmental stochasticity produces an asymmetric distribution of population trajectories, with the 95th percentile extending further over the median than the 5th percentile extends below it (Figure 10-1, top right panel). This asymmetry arises from two distinct mechanisms affecting the upper and lower tails of the distribution differently. The similarity of the 95th percentiles between scenarios with and without density dependence (comparing top right and bottom right panels) likely reflects the ABC calibration process, which adjusted baseline parameters to achieve comparable target population growth rates across model configurations. Consequently, density dependence has limited influence on the upper tail of the distribution. In contrast, the 5th percentiles differ markedly between these scenarios: with density dependence, the worst-case outcomes are less severe because reduced population size means less competition for resources, effectively increasing per-capita resource availability even when environmental conditions are poor. However, this compensatory effect is insufficient to fully offset poor environmental conditions—density dependence can reduce competition but cannot increase the total resource pool. Consequently, iterations experiencing poor environmental conditions (low daily resource draws from the beta distribution) remain below the median, though not as far below as they would be without density dependence. The functional difference between the two configurations becomes more apparent following disturbance, where density dependence allows compensatory recovery by increasing per-capita resource availability as population size declines. The iPCoD DEB model was calibrated using ABC to produce realistic population growth rates in the absence of disturbance. When environmental stochasticity is excluded, resource availability is constant ($R_{\text{mean}} \approx 3.13$), and animals operate closer to their energetic margins. When environmental stochasticity is included, daily resource availability varies around a higher mean ($R_{\text{mean}} \approx 3.39$). The higher mean was necessary during ABC calibration to achieve the same target population growth rate, because on some days animals experience below-average resources and must compensate.

This difference in baseline energetic state has important consequences for how populations respond to disturbance:

- **Without environmental stochasticity:** Animals have less energetic buffer. When disturbance removes foraging opportunities, they are more likely to fall below critical thresholds for survival or reproduction, resulting in larger population impacts.
- **With environmental stochasticity:** Animals have higher average energy intake and build up larger reserves. When disturbance occurs, they have more buffer to absorb the energetic cost, resulting in smaller population impacts.

Both environmental stochasticity and density dependence reduce the predicted impact of disturbance, but through different mechanisms:

- **Environmental stochasticity effect:** Higher baseline Rmean provides additional energetic buffer, reducing the impact of lost foraging time.
- **Density dependence effect:** Compensatory increases in per-capita resources when population declines, facilitating recovery.

When both mechanisms are included, their protective effects do not fully combine additively. Once animals have sufficient energetic buffer from higher Rmean, there is less need for density-dependent compensation, and vice versa. This interaction explains why the combined effect of both mechanisms (e.g., -2% at 5th with fixed 6h disturbance, Table 4-2) is not simply the sum of their individual effects.

4.5 Understanding the effect of the piling schedule on population dynamics

The changes in timing of the piling were tested by comparing the original KEC 5.0 scenario with the three additional modified scenarios described in section 3.3: the 'smoothed' one, the one avoiding August, and the one avoiding September, see section 3.3. The basic scenario is simulated twice (run 1 and run 2, each with 200 iterations) to check the consistency of the calculated 5th percentile using iPCoD DEB. The other scenarios are calculated once, with 300 iterations. All iPCoD DEB calculations for this comparison are without density dependence and without environmental stochasticity.

The 5th and 50th percentiles of the population reduction per model run are shown in Figure 4-5 and Table 4-3.

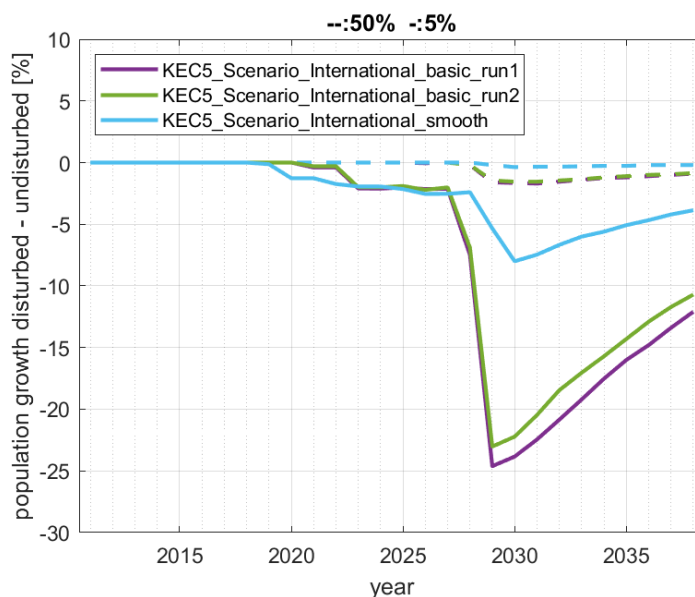


Figure 4-5. 5th (solid lines) and 50th (dashed lines) percentiles of the calculated population reduction (in percent of the total North Sea population of 373,310 porpoises) for the considered piling schedules: the basic KEC 5.0 schedule, a repeat run of the same schedule and the smoothed piling schedule.



Table 4-3. Maximum value of the population decline as percentage of total population, for the various scenarios, with the associated total number of piling days and harbour porpoise disturbance days (HPDD)

Scenario	5th (%)	50th (%)	piling days	HPDD / 1e6
basic_run1	-25	-2	8457	44.9
basic_run2	-23	-2	8457	44.9
smooth	-8	-0.4	8972	45.4

The results show:

- The median (50th percentile) of the calculated population decline is 2% for the basic scenario and further reduced (to 0.4%) for the smoothed scenario.
- The 5th percentiles from the two runs from the basic international scenario are relatively close to each other (difference smaller than 2%), which gives confidence in fairly consistent results regardless of the number of simulations (Figure 4-6). These basic scenarios had the largest effect, with a maximum population reduction of 25% and 23% (Table 4-3).
- The maximum population reduction is significantly lower (8%) for the smoothed piling schedule, despite the slightly greater numbers of piling days and porpoise disturbance days (Table 4-3, Figure 3-2).

It should be noted that the currently parameterised population growth of porpoises in the iPCoD DEB model results in an undisturbed population of which the median size increases over time (Figure 4-6, Figure 10-1). Hence, the starting year for the calculations has an effect on the size of the undisturbed population during the piling years for each model run. The above results were for a calculation window from 2011 until 2038, in which piling first started in 2016. To test the effect of the starting year, additional calculations were carried out for a calculation window from 2016 until 2042, with the same piling schedule starting in 2016, hence excluding the first 5 years from the basic scenario. The piling period was extended until 2034 so that all piling projects were included in all the scenarios. Thus, all the scenarios are for the same total number of piling days and porpoise disturbance days. Figure 4-6 shows the predicted development of the undisturbed population for all scenarios. The population size distribution during the piling years (2016-2034) is different when the calculation window is shifted. Since all undisturbed scenarios are nominally equal, these represent repeated estimations of the population trend. This illustrates the uncertainty (of a few %) in the estimation of the 5th percentiles from 200 models runs for the initial basic scenarios and 300 model runs for the other scenarios, increasing over the years.

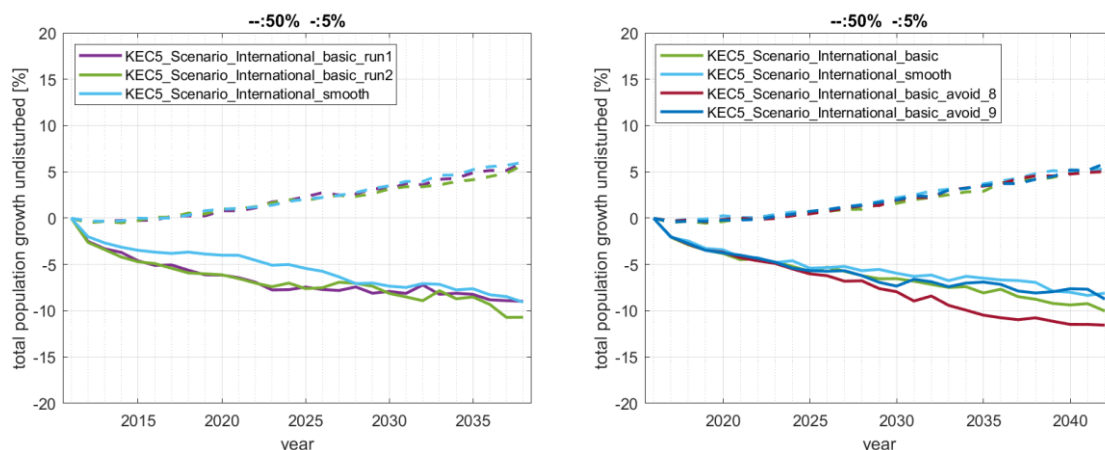


Figure 4-6. 5th (solid lines) and 50th (dashed lines) percentiles of the calculated population reduction (in percent of the total North Sea population of 373310 porpoises) for the undisturbed population associated with the calculations for the various scenarios. Left: calculation window 2011-2038. Right calculation window 2016-2042.

Figure 4-7 and Table 4-4 show the population reduction for the considered scenarios over the calculation window from 2016 until 2042. The total number of piling days and porpoise disturbance days is the same for all four scenarios, but these are differently distributed over the years.

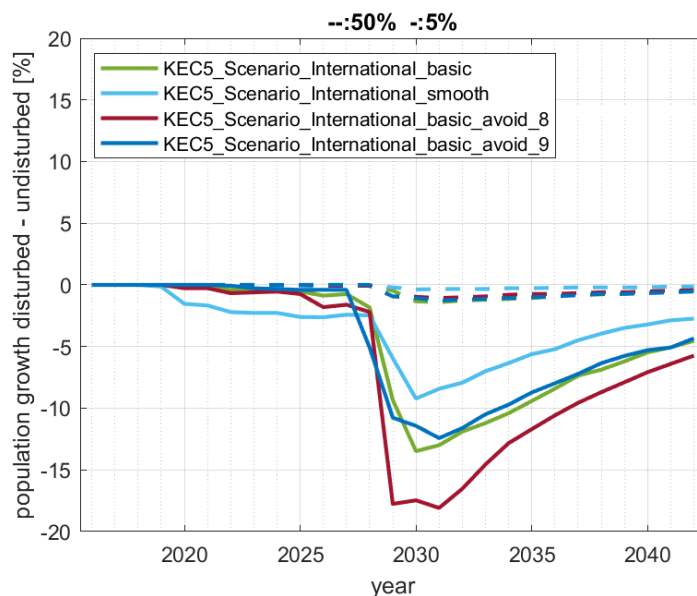


Figure 4-7. 5th (solid lines) and 50th (dashed lines) percentiles of the calculated population reduction (in percent of the total North Sea population of 373310 porpoises) for the considered piling schedules with calculation window 2016-2042: the basic KEC 5.0 schedule, the smoothed schedule and two schedules avoiding piling in August or September.

Table 4-4. Maximum value of the population decline as percentage of total population, for the various scenarios, with the associated total number of piling days and harbour porpoise disturbance days (HPDD), for the calculation window 2016-2042.

Scenario	5th (%)	50th (%)	piling days	HPDD / 1e6
basic	-14	-1	8972	45.4
smooth	-9	-0.4	8972	45.4
basic - avoid August	-18	-1	8972	45.4
basic - avoid September	-12	-1	8972	45.4

Summarising the results:

- The predicted population declines are smaller in comparison to the scenarios where no-piling years were included at the beginning of the simulation (Table 4-3, Table 4-4). Changing the calculation window reduces the maximum 5th percentile population reduction for the basic scenario from 23-25% to about 14%.
- This calculation confirms that the maximum population reduction for the smoothed piling schedule, that avoids the peak in porpoise disturbance days in 2027, remains significantly lower (9%) for the same number of piling days and porpoise disturbance days as the basic scenario.
- The two scenarios designed to study the effect of avoiding disturbance in sensitive months (August and September) show a higher population decline than the basic scenario (Table 4-4) instead of an expected reduction of the population decline.

These results can be better understood when comparing the trends of piling days, harbour porpoise disturbance days (HPDD) and population decline over the years (Figure 4-8). The greatest declines occur in the year after a year in which the number of HPDD peaks. Because the number of disturbed porpoises varies between projects, such a peak does not necessarily coincide with a peak in the number of piling days. The three scenarios have the same total number HPDD but they are differently distributed over the years. The peaks in HPDD differ significantly between the scenarios. The two scenarios avoiding piling in August or September have the highest peaks, due to the choice to compensate for the delay by allowing more simultaneous piling projects than in the basic scenario (Figure 4-8). For the scenario avoiding August this leads to a high annual peak in the number of HPDD, resulting in a greater worst-case (5th percentile) decline than the basic scenario. That indicates that the most likely reason behind larger overall population decline is not avoiding piling in a given month, but the total number of piling days/HPDD in a given year. The median effect (50th %) show neglectable effect on the populations regardless of the scenario tested.

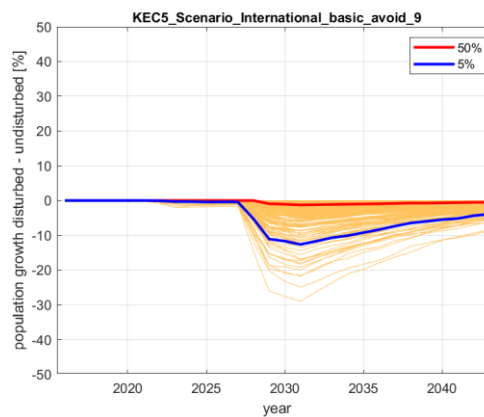
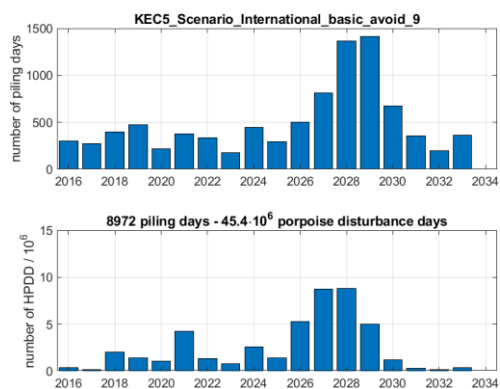
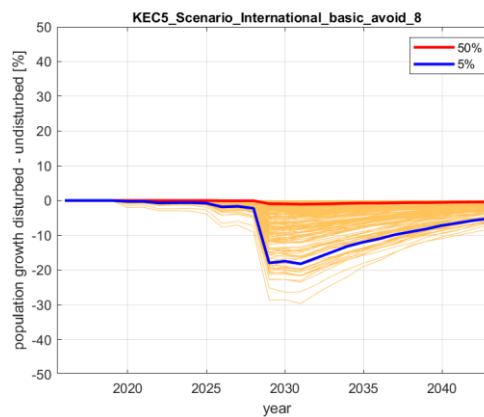
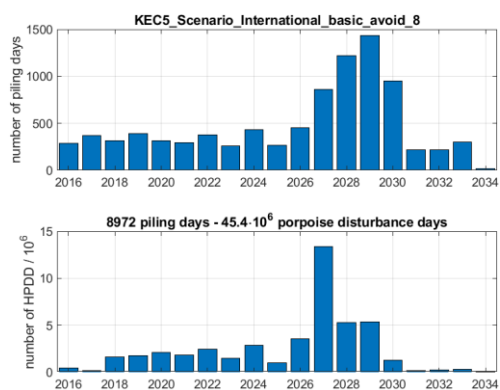
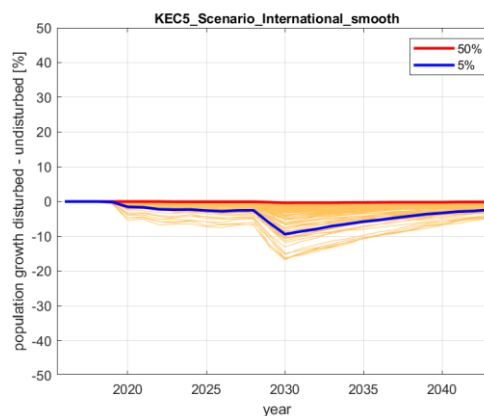
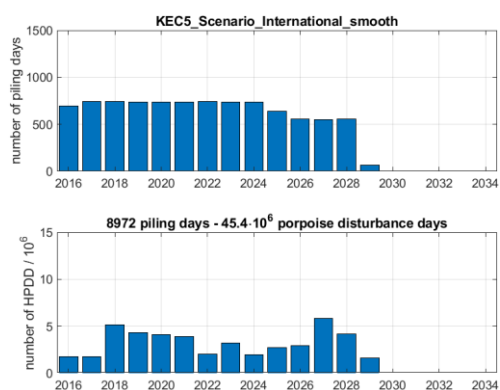
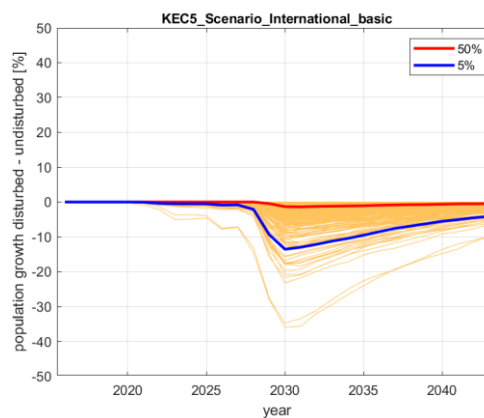
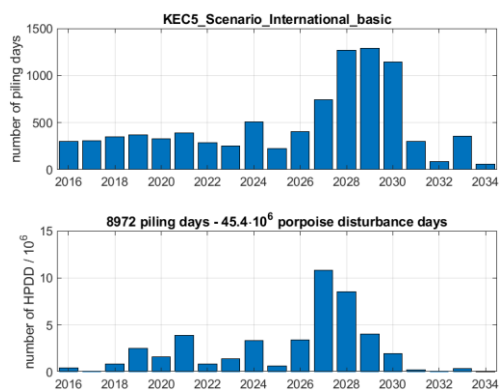


Figure 4-8. Yearly numbers of piling days, harbour porpoise disturbance days (HPDD) and population decline (in percent of the total North Sea population of 373310 porpoises) for the considered piling schedules with calculation window 2016-2024: the basic KEC 5.0 schedule, the smoothed schedule and two schedules avoiding piling in August or September.

4.6 WP3: Linking DEB and iPCoD DEB with the Ecowende/Wozep workshop

Prior to the workshop, we reviewed all the parameters included in the iPCoD DEB and send a list of topics and parameters which may be updated based on the work of workshop participants. The outcome of the workshop and their relation to the iPCoD models are described in detail in Heinis et al. (2026). Short summary and the link between this report and Heinis et al. (2026) is given in Appendix C. Below are the main conclusions.

The workshop confirmed that several of the parameters we had identified as candidates for review are both influential on model outputs and currently constrained by parameterisation rather than direct empirical evidence. Four cross-cutting themes emerged. First, whether harbour porpoises in the North Sea constitute one population or several (sub)populations recurred throughout the workshop but remained unresolved for lack of data; this question is foundational, as it bears on whether region-specific demographic rates are needed, how density dependence should be represented, and how the probability of exposure should be modelled. It is closely related to the consistent evidence for regional as well as seasonal variation in body condition, of which the model currently captures only the seasonal dimension. Second, the ability of animals to compensate for lost foraging, and the assumed duration of foraging cessation, were identified as among the most important and least well-constrained elements of the model, with broad support for revisiting them empirically as data become available. Third, the movement ecology of porpoises in the southern North Sea was repeatedly flagged as a critical knowledge gap underpinning both the probability of exposure and the treatment of repeated disturbance. Fourth, considerable relevant information already exists in stranding and necropsy data, but realising its value requires harmonised diagnosis and terminology across stranding networks — most visibly around the definition of "starvation".

Concrete follow-up actions were mapped against most of these topics across short-, medium- and long-term horizons, providing a route by which these priorities can feed into successive KEC updates. Full details are given in Appendix C.

5 Discussion

5.1 iPCoD EE vs iPCoD DEB

The comparison between iPCoD EE and iPCoD DEB revealed both similarities and important differences in predicted population trajectories. When iPCoD DEB was configured without density dependence and without environmental stochasticity (the settings most comparable to iPCoD EE) the two models produced broadly similar magnitudes of maximum population decline relative to undisturbed scenario at the 5th quantile (–19% for iPCoD EE versus –22% for iPCoD DEB).

A first major difference is the timing of onset of population decline and the capacity for recovery. In iPCoD EE, population decline at the 5th quantile began earlier in the simulation period compared to iPCoD DEB. This earlier onset likely reflects fundamental differences in how the two models translate disturbance exposure into population effects. In iPCoD EE, the expert-elicited transfer functions apply a direct multiplicative effect on vital rates once an individual's cumulative disturbance days exceed a threshold. This relationship is immediate and deterministic: as soon as sufficient disturbance accumulates within a year, survival and fecundity are reduced according to the elicited function. In contrast, iPCoD DEB models disturbance effects through an energetic pathway that introduces temporal lags. Disturbed animals lose foraging time, which creates an energy deficit that first affects and depletes energy-reserves before propagating to vital rates. Furthermore, the bioenergetic framework includes a compensation mechanism whereby animals can increase foraging effort when body condition declines and the resources are sufficient, partially buffering against the immediate effects of disturbance. These mechanistic features delay the manifestation of population-level effects in iPCoD DEB relative to iPCoD EE.

A second major difference between the models concerns population recovery after disturbance ceases. iPCoD EE showed almost no recovery, with the mean 5th quantile remaining at -17% during the six years post-disturbance compared to a maximum decline of -19% during the disturbance period. In contrast, iPCoD DEB demonstrated clear population recovery following the cessation of disturbance, even in the absence of density-dependent compensation (DD not included in calculation). As discussed in Section 4.1, this recovery is driven by disturbance-induced shifts in age structure: the selective mortality of pregnant and lactating females during the disturbance period increases the proportion of immature females, who subsequently mature and reproduce once disturbance ends. iPCoD EE lacks a mechanistic recovery pathway—once vital rates have been reduced by disturbance; there is no process by which individuals can regain lost reproductive potential or by which the population can compensate through age structure effects. These similarities in maximum decline but differences in temporal dynamics between the baseline configurations of the two models are important for regulatory interpretation to define a period over which the disturbance should be evaluated (see Recommendation section).

A third difference is the effect of the use of additional functionality of the iPoC DEB model. When additional model features unique to iPCoD DEB were included, the predicted outcomes diverged more substantially from iPCoD EE. Including density dependence in iPCoD DEB accelerated population recovery and reduced the post-disturbance 5th quantile from -13% to -7%. Including environmental stochasticity had an even larger effect, reducing worst-case impacts to -4% (without DD) or -2% (with DD). The choice of disturbance duration further magnified differences between the models: using an Erlang distribution with a mean of 2 hours (based on empirical estimates of harbour porpoise response durations) reduced the 5th quantile decline to less than 1% under most iPCoD DEB configurations, compared to the persistent -17% decline in iPCoD EE.

These results suggest that iPCoD EE produces more persistent population-level effects primarily due to the absence of a mechanistic recovery pathway and compensatory mechanisms, whereas the bioenergetic framework in iPCoD DEB allows individuals to compensate for lost foraging time once disturbance ends, enabling population recovery irrespective of whether density-dependent mechanisms are included. The magnitude of the difference between the two modelling approaches depends critically on which iPCoD DEB configuration is used, with the inclusion of environmental stochasticity, density dependence, and empirically derived disturbance durations each contributing to reduced predicted impacts relative to iPCoD EE. These findings highlight that the choice of model and model configuration substantially influences predicted population impacts, and that the mechanisms underlying these differences should be carefully considered and assessed when interpreting results for regulatory assessment.

5.2 iPCoD DEB: Sensitivity of the model predictions to presence of density dependence mechanism, environmental stochasticity and duration of disturbance

The coefficient analysis revealed that disturbance duration had the largest influence on predicted population impacts across all percentiles. Reducing disturbance duration from 6 hours to a mean of 2 hours (Erlang 2h) consistently produced the greatest reduction in population impact, particularly for worst-case (5th percentile) scenarios. This is unsurprising, as shorter disturbance duration directly translates to less foraging time lost and therefore smaller energetic deficits. Conversely, introducing variability in disturbance duration while maintaining the same 6-hour mean (Erlang 6h) increased population impacts compared to a fixed 6-hour duration, because some individuals experience disturbance lasting considerably longer than 6 hours.

Environmental stochasticity was the second most important parameter for worst-case (5th percentile) scenarios, substantially reducing the predicted population impact. This effect arises because the ABC-calibrated baseline resource availability (Rmean) is higher when environmental stochasticity is included (~3.39 vs ~3.13), providing animals with greater energetic reserves to buffer against disturbance. For median (50th percentile) and best-case scenarios (95th percentile), environmental stochasticity had a smaller or even slightly negative effect, reflecting the increased spread of outcomes when additional sources of variation are included.

Density dependence had a moderate protective effect across all scenarios by allowing compensatory increases in per-capita resource availability when populations decline. However, its relative importance was generally lower than that of disturbance duration and environmental stochasticity, suggesting that the immediate energetic impacts of disturbance (determined by duration and baseline resource levels) are more influential than longer-term compensatory mechanisms in shaping population outcomes.

The sensitivity analysis presented here differs from a classical sensitivity analysis in which each parameter is varied by a consistent proportion (e.g., $\pm 5\%$ of its baseline value) to enable direct comparison of parameter influence on model outputs. In our analysis, two of the three factors examined (density dependence and environmental stochasticity) are implemented as binary switches (included or excluded) rather than as

continuously variable parameters. The underlying parameters governing these processes were calibrated through Approximate Bayesian Computation (ABC) to produce realistic undisturbed population dynamics and cannot be independently varied without compromising the biological validity of the model. Consequently, the "effect" of including or excluding these processes represents a qualitative structural change to the model rather than a quantitative perturbation of a specific parameter value. The third factor (duration of disturbance) was varied across three scenarios (fixed 6 hours, Erlang with mean = 2 hours, and Erlang with mean = 6 hours), but these values were not selected to represent equivalent proportional changes. Our results suggest that the choice of disturbance duration had the largest influence on predicted population impacts, followed by environmental stochasticity. However, this ranking is contingent on the specific parameter values tested; had we used an intermediate value (e.g., Erlang with mean = 4 hours), the relative importance of disturbance duration compared to the other two parameters might have been reduced. These limitations should be considered when interpreting the sensitivity analysis, and the results should be viewed as illustrative of how different model configurations affect outcomes rather than as a formal quantification of parameter sensitivity.

5.3 iPCoD DEB: Sensitivity of the model predictions to timing of disturbance

The piling schedule simulations revealed that worst-case (5th percentile) population outcomes are highly sensitive to the temporal distribution of disturbance, whereas median (50th percentile) outcomes remained consistently small (<2%) across all scenarios tested. The most striking finding was that the predicted worst-case population decline was strongly driven by the presence of annual peaks in the number of harbour porpoise disturbance days (HPDD). The basic KEC 5.0 scenario, which features a pronounced peak in HPDD in 2027, produced worst-case declines of 23–25%, whereas the smoothed scenario—which distributed the same total number of piling days and HPDD more evenly across years—reduced the worst-case decline to just 8%. This represents a threefold reduction in predicted impact despite a slightly higher total number of piling days in the smoothed scenario.

The importance of annual peaks is further illustrated by the scenarios designed to avoid piling in sensitive months. Contrary to expectations, avoiding August resulted in a higher worst-case decline (18%) than the basic scenario (14% when using the same calculation window), while avoiding September produced a slightly lower decline (12%). These counterintuitive results occurred because the piling scenario generation algorithm compensating for the avoided months included more simultaneous piling projects than the original KEC 5.0 scenario, which created new peaks in HPDD that exceeded those in the basic scenario. This demonstrates that the annual distribution of disturbance days—specifically the avoidance of years with exceptionally high cumulative disturbance—is a more important determinant of worst-case population outcomes than avoiding specific months within the annual cycle.

The simulations also highlighted the sensitivity of results to the calculation time window. Including a five-year period without piling at the beginning of the simulation (2011–2015, so called 'burn-in' period) inflated the

worst-case population decline from 14% to 23–25% for the basic scenario. This occurs because the iPCoD DEB model is parameterised to produce population growth from the first year of simulation; consequently, the growing undisturbed population during the burn-in period creates a higher baseline against which disturbance effects are measured, artificially amplifying the apparent impact. These findings suggest that assessments should begin simulations at the onset of piling activity rather than including pre-disturbance years.

The intended analysis of which months should be avoided to minimise population impacts could not be completed as planned. To isolate the effect of avoiding specific months, the total number of piling days and HPDD must remain constant across scenarios. However, maintaining these constraints while avoiding certain months necessarily alters the annual distribution of disturbance, introducing confounding factors that obscure the effect of seasonal timing. Future analyses specifically designed to test seasonal sensitivity—potentially using simplified or hypothetical piling schedules—would be required to address this question directly. However, such analysis would not be informative for KEC 6.0, which is based on the analysis of multiple simultaneously constructed projects.

6 Recommendations

The findings of this assessment have consequences for how iPCoD DEB is configured and interpreted in a regulatory context. Rather than prescribing a single "correct" model configuration, this section describes the implications of particular choices around assessment metrics, model realism and disturbance duration, so that assessors and regulators can make these choices with full awareness of their effects on predicted population outcomes. Based on the findings of this assessment, the following recommendations and considerations are, therefore, made

6.1 Reassessing metrics for quantifying population effects.

Population-level effects in iPCoD DEB (and iPCoD EE) are quantified as the difference between matched pairs of impacted and unimpacted populations, summarised across simulations using percentiles (typically the 5th, 50th and 95th) and evaluated over a defined time window. The most recent version of iPCoD DEB ensures that matched pairs experience identical environmental and demographic stochasticity within each simulation, consistent with the iPCoD EE approach; this enables the same set of summary metrics to be applied to both models. However, the choice of percentile and the choice of time window each have substantial consequences for the magnitude, and in some cases the sign, of the reported effect.

Choice of percentile. The ecological standard currently applied in the Netherlands (Ministry of Economic Affairs 2015) requires that it be possible to establish, with 95% confidence, that the NL population will not decline by more than 5% as a result of NL offshore wind farm construction — i.e. it relies on the 5th percentile of the distribution of simulated population reductions. Analysis of iPCoD DEB outputs shows that simulations producing the largest (worst-case) declines are consistently associated with specific combinations of physiological



parameters — in particular, high basal metabolic rate multipliers (Sigma_M) paired with low mean resource availability (Rmean). These combinations sit in the tails of the parameter distributions produced by the Approximate Bayesian Computation calibration and are consistent with observed population growth rates in the absence of disturbance, but they represent the edges of the calibrated parameter space rather than the most probable states of the real system. The consequence is that the 5th percentile reflects parameter uncertainty at least as much as it reflects ecological worst-case conditions: as uncertainty in key physiological parameters narrows (e.g. through empirical work on harbour porpoise energetics), the 5th percentile would be expected to move closer to the median. The median (50th percentile), by contrast, reflects the central tendency of the simulated system given current knowledge, and represents the most probable population response under the modelled conditions. It is not an uncertainty-free estimate — it remains conditional on the assumed parameter distributions and model structure — but it is less sensitive than the 5th percentile to the shape of those distributions. The consequence of continuing to rely exclusively on the 5th percentile is that reported impacts will remain dominated by parameter uncertainty; the consequence of reporting the median (50th percentile) alongside the 5th percentile is that both the most probable outcome and the worst-case outcome under current uncertainty are made visible to decision-makers.

Choice of time window. Under the current KEC framework, the population reduction is evaluated as an average over a six-year period beginning after the final piling operation is completed. This window was defensible in the context of iPCoD EE, where population size stabilises (without recovery) once disturbance ends; a fixed post-disturbance window in that case captures a relatively stable quantity. The same is not true of iPCoD DEB. In iPCoD DEB the population can recover after disturbance ends, even in the absence of density dependence (through disturbance-induced shifts in age structure) and more strongly when density dependence is included. The magnitude of the modelled decline therefore fluctuates over time rather than stabilising, and the value reported for a fixed six-year window is sensitive to exactly where in the recovery trajectory that window falls. The consequence is that a fixed post-disturbance window can either over- or under-estimate the maximum population effect, depending on the scenario and on whether density-dependent compensation is active. Reporting additional quantities — for example the minimum population size (i.e. the deepest point of the trough) and the population size at a fixed endpoint — provides a fuller characterisation of the disturbance effect and avoids this sensitivity.

6.2 Inclusion of density dependence and environmental stochasticity

iPCoD DEB allows the user to switch density dependence and environmental stochasticity on or off. These are not cosmetic choices: they materially change the predicted magnitude of population-level impacts, because they change the biological realism of the simulated populations.

Density dependence. When density dependence is switched on, the population can partly compensate for disturbance-driven declines through increased per-capita resource availability as the population falls below

carrying capacity. When it is switched off, no such compensation is possible, and the population cannot recover through this pathway. The consequence of disabling density dependence is therefore that predicted declines are larger and recovery is slower (or absent), but this is not an artefact of the model — it reflects a configuration in which a real ecological process has been removed.

Environmental stochasticity. When environmental stochasticity is switched on, daily resource availability fluctuates around its mean, and animals tend to accumulate larger energetic reserves to buffer against these fluctuations (because the model is calibrated against observed population growth rates under this variable regime). When it is switched off, resources are constant and animals operate closer to their energetic margins. The consequence of disabling environmental stochasticity is therefore that disturbance has a larger per-individual effect, because the same foraging loss is applied to animals with smaller reserves.

Both features reflect genuine biological processes — compensatory density dependence and day-to-day environmental variability both exist in the real North Sea. Switching them off in a simulation does not produce a more precautionary or more conservative estimate of a real-world effect; it produces an estimate of what the effect would be in a world without these buffering mechanisms.

6.3 Disturbance duration

The default assumption of six hours of foraging cessation per disturbance event has remained unchanged since the second expert elicitation in 2018 (van Beest et al. 2018, Booth et al. 2019). The sensitivity analysis in this study shows that disturbance duration has the largest influence on predicted population impacts of any parameter tested, with disturbance duration interacting with both density dependence and environmental stochasticity. The consequence of this is that the six-hour default is one of the single most important determinants of the magnitude of predicted effects in any iPCoD DEB assessment, and that uncertainty in this value propagates more strongly into population-level predictions than uncertainty in almost any other parameter. Changes in the evidence base for this value — whether from acoustic telemetry, PAM, behavioural response studies or captive work — would therefore be expected to produce correspondingly large changes in predicted outcomes. For as long as the six-hour value is retained as the default, reported population effects should be understood as conditional on this assumption rather than as intrinsic properties of the scenarios modelled.

6.4 Consultation with offshore wind developers

Our findings demonstrate that worst-case population outcomes are strongly influenced by the temporal distribution of piling activity, particularly the presence of annual peaks in harbour porpoise disturbance days. For large-scale cumulative assessments such as KEC, which aggregate the effects of multiple offshore wind farm projects across the North Sea, the scheduling decisions of individual developers combine to create the overall disturbance pattern experienced by the population. The smoothed piling scenario—which distributed

disturbance more evenly across years—reduced the worst-case population decline from 23–25% to 8% despite a slightly higher total number of piling days, demonstrating the substantial benefits that could be achieved through coordinated scheduling.

These results highlight the need for broader discussion and coordination among offshore wind developers, regulatory authorities, and relevant stakeholders regarding the timing and sequencing of construction projects. Currently, individual projects are planned and permitted largely independently, with limited consideration of how their combined schedules affect cumulative population impacts. Our analysis suggests that strategic coordination to avoid years with exceptionally high cumulative disturbance could substantially reduce predicted worst-case impacts without necessarily reducing the total number of projects or piling days.

7 Roadmap for further model development and testing

7.1 Model parameterisation

The current ABC parameterisation results in a population that increases slightly over time in the absence of any type of disturbance (~1% per year). Future work could explore alternative parameterisations that produce more stable long-term population dynamics, which may better reflect equilibrium conditions where density-dependent mechanisms more strongly regulate population growth. Re-parameterisation may also be warranted if new empirical data on harbour porpoise energetics, behaviour or demography become available, for example from ongoing projects such as the Ecowende initiative and the Wozep programme. Suggested parameters are energy expenditure (Sigma_M), and different demographic rates. As shown reducing parameter uncertainty through empirical research on harbour porpoise energetics could substantially narrow the range of predicted outcomes, potentially leading to more robust and defensible population assessments. This task would not require any code modifications, but it would require a large number of simulations.

7.2 Revisiting disturbance duration

The default assumption of 6 hours of foraging cessation per disturbance event has remained unchanged since the second expert elicitation in 2018 (van Beest et al. 2018, Booth et al. 2019). Our sensitivity analysis demonstrates that disturbance duration has the largest influence on predicted population impacts of all parameters tested. Given the importance of this parameter, a systematic review of recent empirical data on harbour porpoise behavioural responses to pile-driving noise is recommended to determine whether updated estimates of disturbance duration are warranted. This task would not require any code modifications, as the option of changing duration is already available in the code.

7.3 Seasonal timing of disturbance

The sensitivity analysis in this report could not isolate the effect of avoiding piling in specific months, because the algorithms used to redistribute piling across the remainder of the year introduced new annual peaks in HPDD



that confounded the seasonal signal. A dedicated analysis — using simplified or hypothetical schedules in which total HPDD is held constant while seasonal distribution is varied — would be required to address this question directly. This was not attempted in the current work because it would not inform KEC 6.0, which is built around multi-project scenarios; however, it would be valuable for informing project-level mitigation measures and for understanding how the energetic cycle of harbour porpoises maps onto population-level vulnerability. This task would not require any code modifications.

8 Acknowledgements

We would like to thank you Wozep/Ecowende programme for enabling SMRU Consulting, HWE and TNO for participation in the workshop and all the workshop participants for a great discussion.

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10 Appendix A

10.1 Code performance

The main optimizations implemented between the original and current code involve vectorization of the daily simulation loop. In the original code, each daily time step included an explicit loop over all alive individuals, processing each female's energy intake, maintenance costs, body condition, lactation, and calf calculations one at a time. The optimised code eliminates this inner loop by using vectorized R operations that process all individuals simultaneously in a single operation. Only processes that require sequential random number generation or have complex conditional side effects (e.g. pregnancy and starvation death checks) retain small loops, but these iterate only over the subset of affected individuals rather than the entire population. Additional vectorization was applied to the disturbance probability calculations in the code simulating the initial population structure and disturbance settings, replacing nested loops with matrix multiplication and sum operations. Additionally, we made sure that values which are calculated multiple times in the code but do not require recalculation, are now calculated only once and stored for the rest of the simulation. These modifications resulted in simulations running 5-10 times faster depending on the simulation settings (see more details below).

Based on the discussion with TNO and Rijkswaterstaat, the model was further modified to align with the modelling approach of iPCoD EE (see more details in the next section). In that model, the matched pairs of impacted and unimpacted populations experience the same environmental and demographic stochasticity within one simulation of the model. Implementing these changes to iPCoD DEB resulted in further improvements in code performance. The disturbed population is only simulating individuals affected by disturbance and not the entire population (as was the case when disturbed and undisturbed populations were simulated independently).

An example of the final simulations of an undisturbed population is given in Figure 10-1. The iPCoD DEB model was parameterised to simulate a population of the harbour porpoise increasing slightly with time (Harwood et al. 2020b). The average population growth varied between 5-8% over 30 years of simulation, depending on the model configurations.

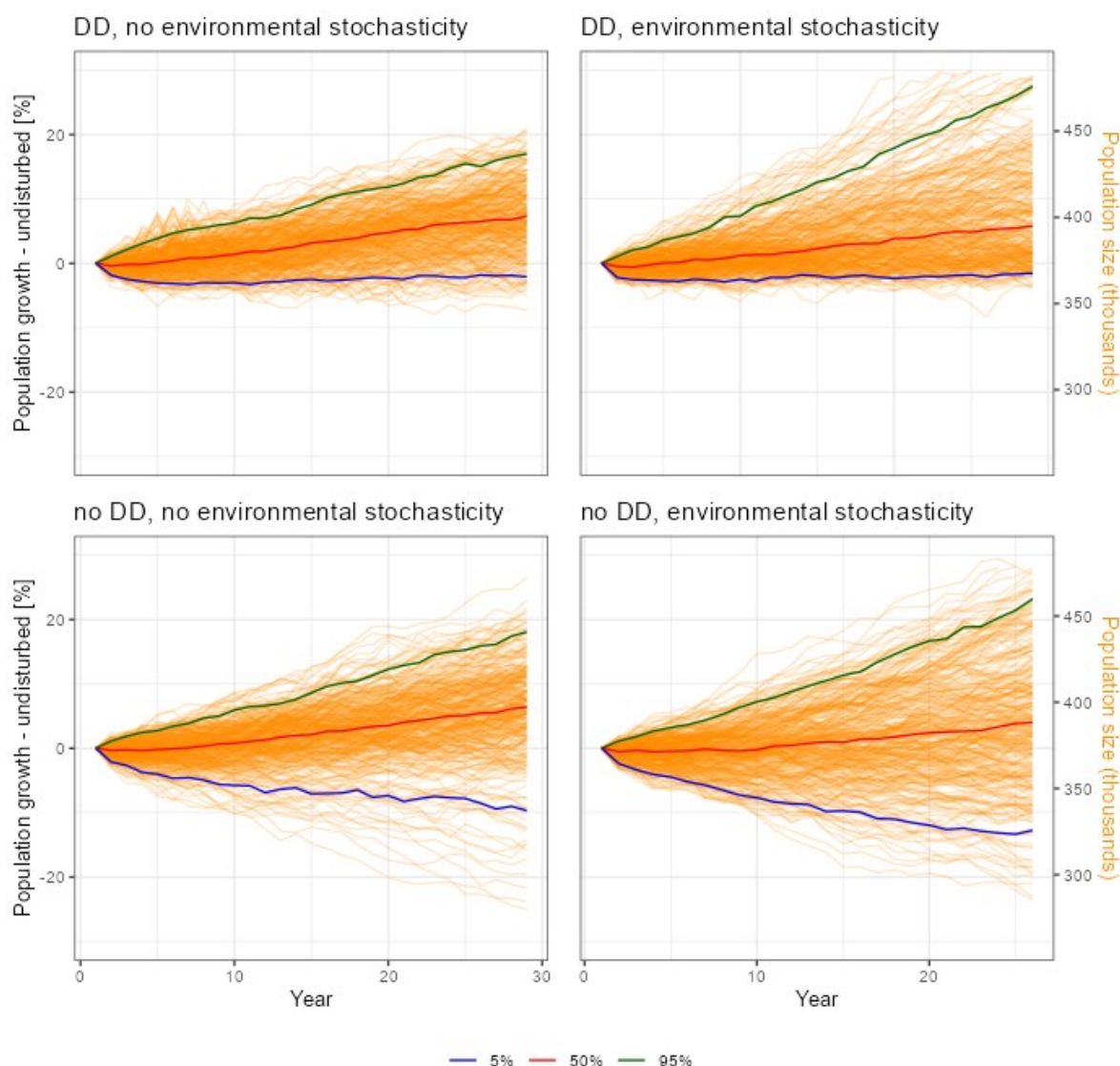


Figure 10-1. Undisturbed harbour porpoise population dynamics shown as individual trajectories (orange lines, 300 iterations) with corresponding 5th (blue), 50th (red), and 95th (green) percentiles of population growth. Panel titles indicate model configuration: presence or absence of density dependence (DD) and environmental stochasticity.

A range of simulations were then performed to understand which input parameters have the highest effect on code performance. The computational time of the iPCoD DEB simulation is primarily determined by the nested loop structure, where daily calculations are performed for all living individuals across all simulated years, repeated for each bootstrap iteration. The number of bootstrap iterations (nboot) has a direct linear effect on runtime, as the entire simulation (both undisturbed and disturbed populations) is re-run for each iteration. The number of simulated years (years/total_years) also has a linear effect on runtime, but with an additional compounding factor: as the simulation progresses, surviving female calves are recruited into the adult population, causing the number of tracked individuals to grow over time and making later years more computationally expensive than earlier ones. The initial number of simulated females (sim_number) has a linear



effect on the daily vectorized operations (energy intake, maintenance costs, body condition calculations), though this effect is moderated by the efficiency gains from vectorization. The number of years with piling activity (*pile_years*) has a relatively minor effect, as it only adds disturbance-specific processing on top of the base simulation that runs regardless of disturbance. However, the number of years with piling activity usually defines the number of simulated years. The actual number of piling days per year (determined by the piling schedule) has a moderate effect, as the disturbance processing loop iterates over each day with active piling within a year. Similarly, higher number of disturbed individuals (*numDt*) result in more individuals being disturbed on each piling day, increasing the processing required for *R_sim* (derived from *Rmean*) modifications and PTS calculations (if included). The number of vulnerable subpopulations (*nvulnmean*) has a small effect, adding a loop over subpopulations (if included) during disturbance processing. The number of piling operations (*pilesx1*) and the number of seasons have negligible impact on runtime, as these parameters only affect the pre-processing stage in *MakelnitScenario* where disturbance probabilities are calculated once per bootstrap iteration, rather than influencing the main daily simulation loops.

The above paragraph is summarized in Table 10-1.

Table 10-1. Model parameters and their effect on the speed of simulations ranked from having highest to lowest effect.

Rank	Parameter	Effect	Description
1	number of bootstrap iterations (<i>nboot</i>)	High, Linear	Entire simulation re-runs for each iteration
2	number of simulated years (<i>years/total_years</i>)	High, Linear and compounding	More years plus population growth increases individuals tracked
3	initial number of simulated females (<i>sim_number</i>)	High, Linear	All daily vectorized operations scale with population size
4	Actual piling days per year	Moderate	Disturbance loop iterates over each active piling day
5	number of years with piling activity (<i>pile_years</i>)	Low-moderate	Adds disturbance processing for years with piling
6	disturbance probability (<i>numDt</i>)	Low-moderate	Higher values mean more individuals processed per disturbance day
7	number of vulnerable subpopulations (<i>nvulnmean</i>)	Low	Adds loop over subpopulations during disturbance processing
8	number of piling operations (<i>pilesx1</i>)	Negligible	Only affects pre-processing matrix dimensions
9	number of seasons (<i>seasons</i>)	Negligible	Only affects NDt/NPt matrix setup in pre-processing

We also added an option to run simulations in parallel computing. While parallel computing can theoretically speed up simulations by distributing bootstrap iterations across multiple CPU cores, it does not always result in faster execution and is not recommended for inexperienced users for several reasons. First, parallel performance is highly machine-dependent, varying with the number of available cores and RAM capacity. Second, there is overhead associated with setting up parallel workers, distributing data to each core, and collecting results afterwards; for simulations with relatively short individual iteration times, this overhead can outweigh the

benefits of parallelisation. Third, R's parallel framework requires sufficient memory to duplicate large data objects (matrices storing population states, disturbance records, etc.) across workers, and when simulations involve many years (>20) or many iterations (nboot >50), memory allocation failures become common, causing individual iterations to fail silently or crash. Fourth, optimal core usage is counterintuitive: testing suggests that using 5–10 cores is more efficient than using all available cores (e.g., 24), because excessive parallelisation leads to memory contention, increased garbage collection, and diminishing returns. Finally, debugging parallel code is considerably more difficult than sequential code, as error messages from individual workers may be suppressed or unclear, making it challenging for inexperienced users to diagnose problems. For these reasons, sequential execution remains the default and recommended approach.

10.2 Code debugging

During the development of the iPCoD DEB model and frequent conversation with TNO, several bugs were identified and fixed to ensure accurate simulation of disturbance effects on marine mammal populations. The most significant issue was the piling schedule bug, where incorrect column referencing meant the model only read six piling operations instead of all operations listed (132 in case of the KEC 5.0 scenario), resulting in only a fraction of the intended disturbance being applied. Additionally, orphaned calves were not being processed correctly after their mothers died — their reserves were frozen and survival was based on random numbers drawn at conception rather than actual body condition. Several inconsistencies between the disturbed and undisturbed simulations were also identified: pregnancy outcomes used different random draws causing populations to diverge even without disturbance, female starvation mortality only occurred in the disturbed scenario during piling years, calf survival was measured using different metrics, and indirect effects on calves (reduced milk intake from disturbed mothers) were lost when calves transitioned to adulthood. All major bugs have been fixed to ensure that the only difference between the disturbed and undisturbed populations is the disturbance itself, allowing valid comparison of scenarios.

The summary of the fixed bugs is given in Table 10-2.

Table 10-2. Summary of bugs identified in the first version of the model with their description and the results (severity) on the model results.

Bug	Severity	Description	Solution
Piling schedule	MAJOR	Model only read 6 of 132 operations due to incorrect column referencing	Fixed column referencing to check all operations
Pregnancy stochastic draws	MAJOR	Different random draws in disturbed scenario caused populations to diverge even without disturbance	Disturbed now uses same values as undisturbed
Orphaned calf survival	MAJOR	Orphaned calves became "ghosts" with frozen reserves; with survival predetermined at conception	Orphans now forage independently and survive/die based on actual body condition



Calf reserve transfer	MAJOR	Only directly disturbed calves had reserves transferred to adulthood; indirect effects lost	All calves now transfer their actual reserves
Female starvation mortality	MEDIUM	Only the disturbed scenario (during piling years) had female starvation	Both scenarios now check starvation every day
Calf survival metric	MEDIUM	Undisturbed used predetermined life expectancy; disturbed used actual survival	Both now use actual survival (calf_age > 0)
Calf starvation age threshold	MINOR	Calves ≤ 5 days could not die from starvation in disturbed but could in undisturbed	Not fixed (negligible impact)

A list of model diagnostics was performed to ensure that the model does simulate as expected, and that the results emerge for the right reason. These model diagnostics were based on simulations of disturbed populations assuming KEC 5.0 international scenarios.

Model testing revealed that simulations resulting in substantial population declines were driven by a combination of increased disturbance exposure and reduced capacity to cope with disturbance. Each simulation draws parameter values from an ABC posterior distribution (Chudzińska et al. 2024), where different parameter combinations produce equivalent population growth and birth rates in the absence of disturbance. These parameters are kept constant for a given simulation and apply equally to disturbed and undisturbed simulations. Figure 10-2 shows population trajectories from simulation of the KEC 5.0 international scenario. The effect of density dependence and environmental stochasticity is not included in this model simulation. Although on average the piling scenario has very little effect on the population (red line), the 5th quantiles show a decline around 20% as its maximum (blue line). As shown by the orange lines, this large decline applied only to few simulations (~7% of all iterations).

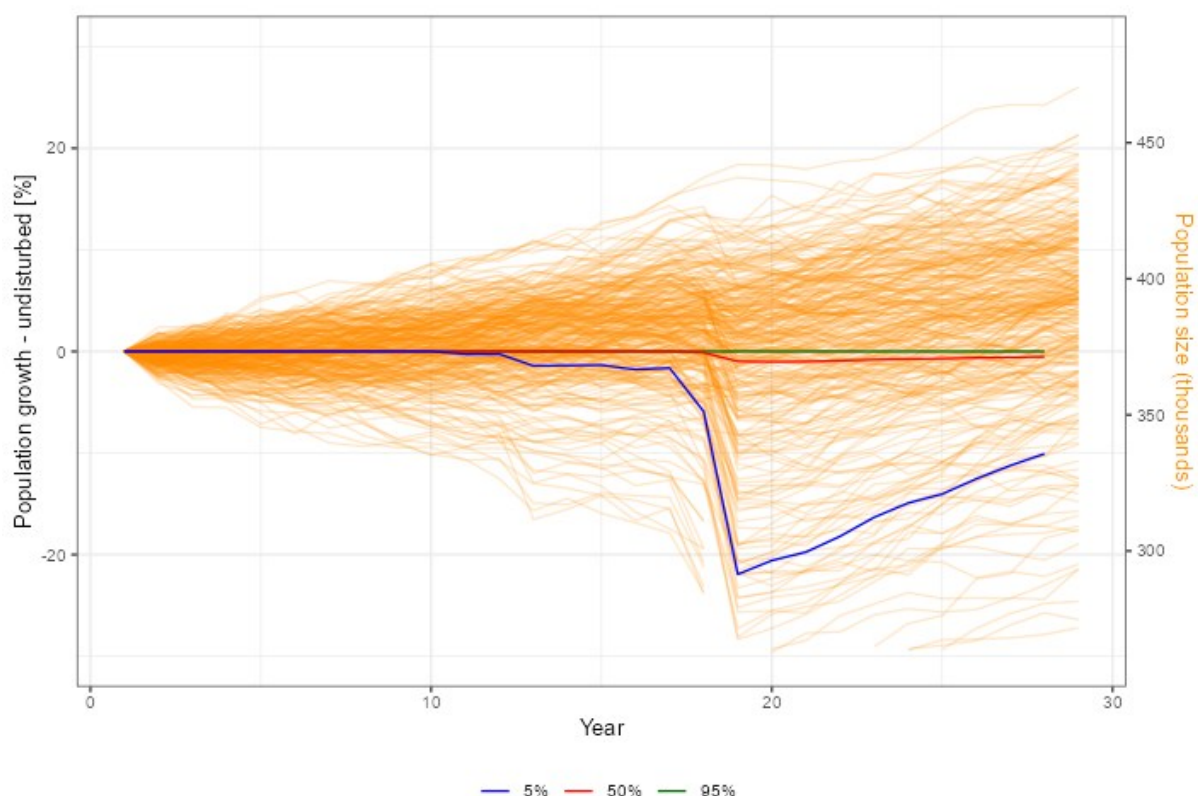


Figure 10-2. Disturbed harbour porpoise population dynamics shown as individual trajectories (orange lines, 300 iterations) with corresponding 5th (blue), 50th (red), and 95th (green) percentiles of changes in the population growth or decline between disturbed and undisturbed population. The effect of density dependence and environmental stochasticity is not included in this model simulation. Piling occurred between years 6 and 21 of the simulations. The last 7 years of simulations is a post-piling period. Note that the plotted year 1 of the simulations represent modelled population at the very beginning of the simulations. All the other years show population size at the end of the simulated year so after applying mortality and accounting for offspring being born that year. Hence all simulations start from the same point at year 1.

The simulations yielding the largest population declines (5th percentile, worst-case scenarios) were characterised by high basal metabolic rate multipliers (Sigma_M) coupled with relatively low resource availability (Rmean) (Figure 10-3). A high basal metabolic rate multiplier increases energy expenditure and thus requires greater energy intake to maintain energy balance. While these parameter combinations produce the target population growth rate in undisturbed conditions, they leave animals with minimal energetic buffer to cope with reduced foraging time during disturbance events.

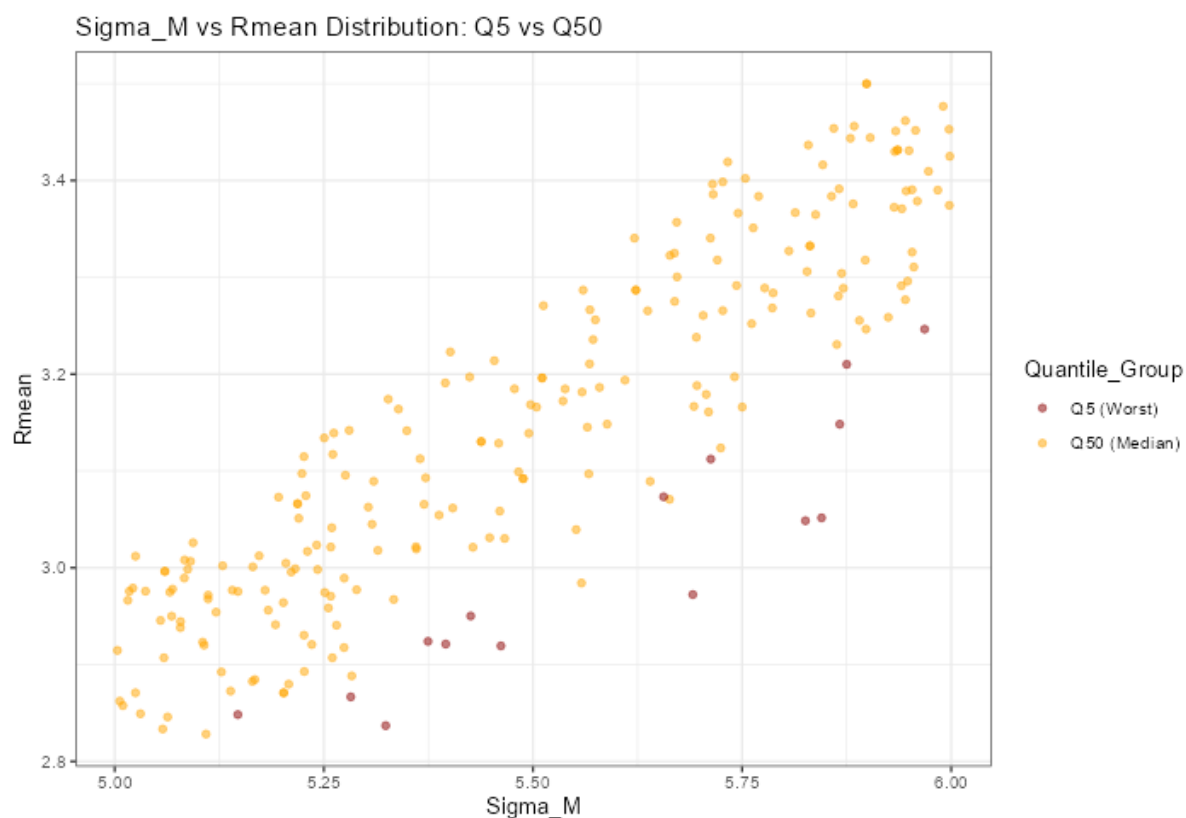


Figure 10-3. Relationship between basal metabolic rate multipliers (Sigma_M) and resource availability (Rmean). 5th percentile, worst-case scenarios (red dots) show lowest Rmean values coupled with relatively high Sigma_M.

Notably, populations in the worst-case scenarios showed recovery after disturbance stopped (year 21 of the simulations), even in the absence of density dependence (Figure 10-2). This counterintuitive result can be explained by disturbance-induced shifts in age structure: pregnant and lactating females experience the greatest energetic deficits and elevated mortality, while immature females (ages 1–5), who do not yet bear reproductive costs, are least affected. Consequently, the proportion of immature females increases during the disturbance period. When disturbance ends, these immature females mature and begin reproducing, leading to an increase in births and subsequent population recovery (Figure 10-4).

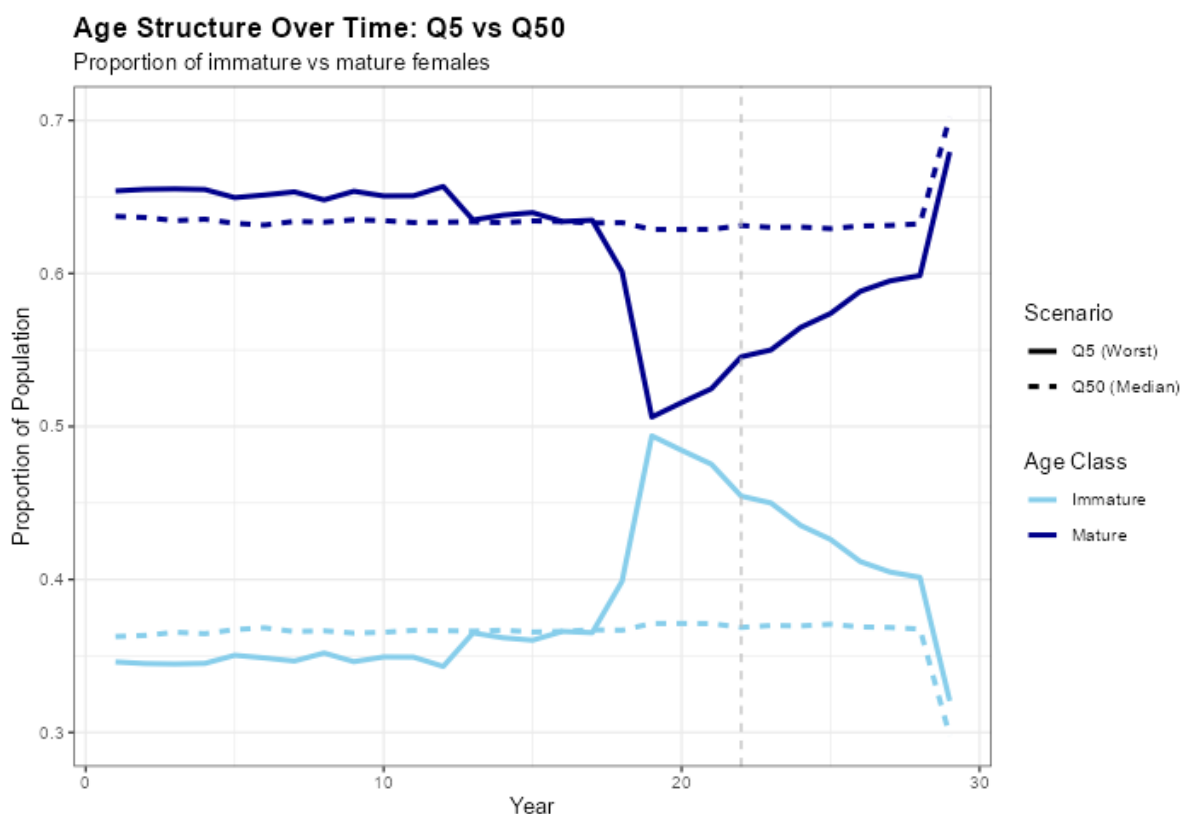


Figure 10-4. Proportion of immature and mature females over 21 years of simulation of disturbance and 7 years of post-disturbance for the simulations from 5th (Q5, worse case) and 50th (Q50, median) quantiles of the 300 iterations. Piling occurred between years 6 and 21 of the simulations. The last 7 years of simulations is a post-piling period. The grey dotted line shows the first year after disturbance stops.

These findings have implications for the interpretation of worst-case scenarios in population assessments, as the 5th percentile outcomes are driven by specific parameter combinations that may warrant further empirical investigation, particularly regarding basal metabolic rate variation in harbour porpoises.



11 Appendix B

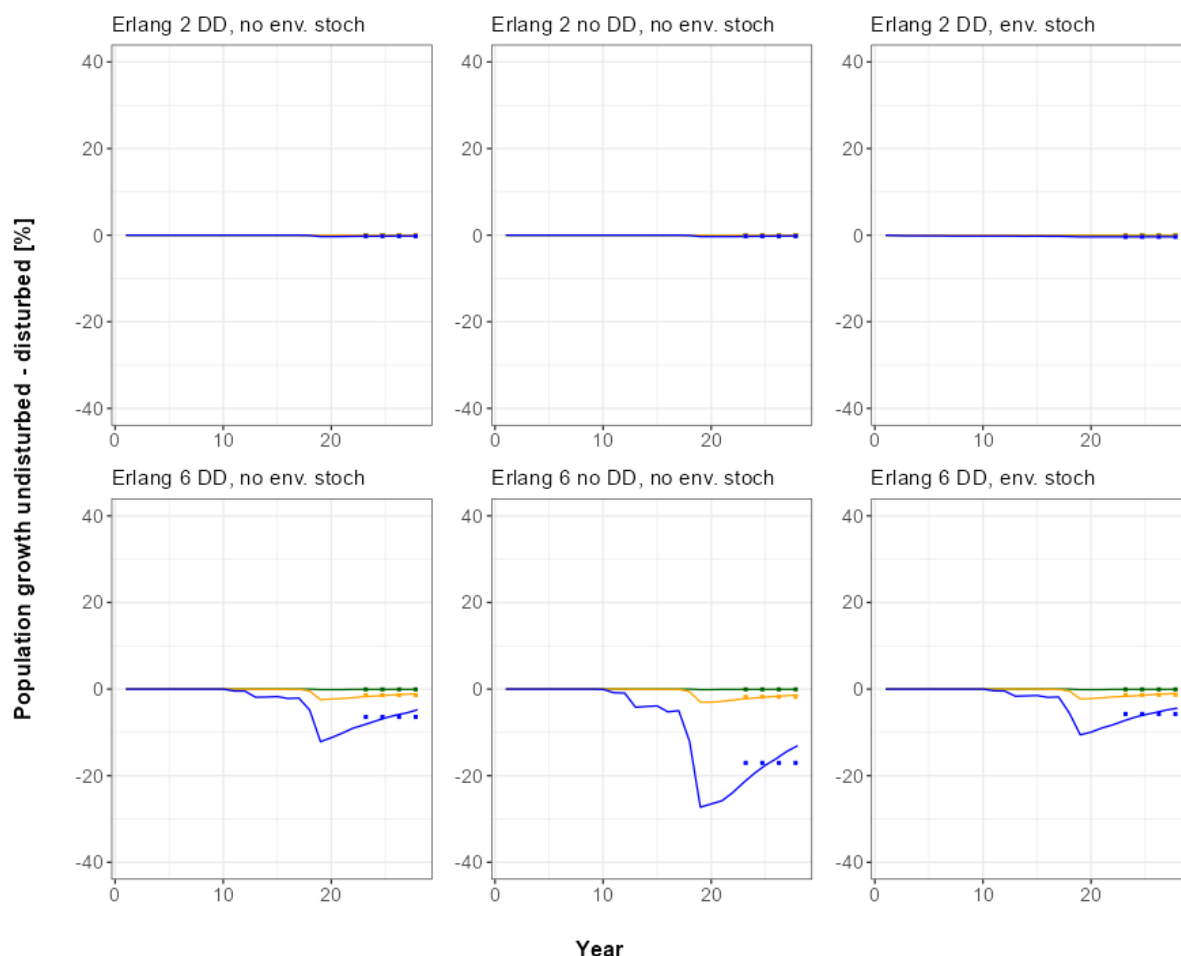


Figure 11-1. Comparison of the percent difference between disturbed and undisturbed harbour porpoise populations over a 28-year simulation period for iPCoD DEB using alternative, to default fixed 6h, duration of disturbance drawn from an Erlang distributions using mean values of 6h (Erlang 6) and 2h (Erlang 2). Lines represent the 5th (blue), 50th (orange), and 95th (green) quantiles across simulations. Dashed lines show mean quantiles over the six years after disturbance ceased to align with approach used in KECs. iPCoD DEB model configurations vary by inclusion of density dependence (DD) and environmental stochasticity (env. stoch). Piling occurred between years 6 and 21 of the simulations. The last 7 years of simulations is a post-piling period.

12 Appendix C

In November 2025, a group of 30 international experts from science, conservation and policy met at the Faculty of Veterinary Medicine of Utrecht University for a three-day workshop organized by Ecowende, University of Utrecht and Rijkswaterstaat (Wozep programme), focusing on the condition of harbour porpoises in relation to offshore wind energy. In this section we present a list of candidate topics suggested to be raised/discussed during the workshop. We also describe how and if these topics were discussed at the workshop. These topics were used to shape the pre-workshop webinar as well as the content of the workshop itself. The outcome of the workshop and in-depth discussion is presented in Heinis et al. (2026).

Prior to the workshop, we reviewed all the parameters in the iPCoD EE and iPCoD DEB models to arrive with a list of topics linked to a given parameter as a candidate to review/discuss during the workshop. Below we list the parameters and briefly summarise how a given topic was discussed or not at the workshop.

1. Demographic rates and age (stage) specific survival rates

Currently the model is parameterised to fixed demographic rates for the entire North Sea population as recommended by Sinclair et al. (2020) based on data in Winship et al. (2008). It was discussed at the workshop that these rates may not be uniform for the entire North Sea, or there may be more than one population in the North Sea.

Question posed at the workshop: Should region specific demographic rates be used in the model?

How it was addressed at the workshop: This topic was addressed in Part I of the workshop, principally in the talk on the life history of harbour porpoises by Lonneke IJsseldijk (section 3.1.1 of Heinis et al. 2026). The presentation drew on necropsy data from stranded and bycaught animals to highlight the large variation in pregnancy rate reported across the species' range, and the regional differences in this and other demographic parameters around the North Sea. The accompanying presentations by Sanne Hessing (on ageing methods, section 3.1.2) and Magnus Wahlberg (on age- and seasonally related changes, section 3.1.3) reinforced the point that the initial age structure and the immature-to-mature ratio are powerful, and currently poorly constrained, metrics for the model. The general discussion on life history (section 3.1.4) concluded that the juvenile/adult ratio is an important metric for modelling and that age distribution from stranding data could help refine adult mortality rates, provided the representativeness of strandings data is assessed.

No firm conclusion was reached on whether harbour porpoises in the North Sea should be treated as a single population with uniform vital rates, or as several (sub)populations with variable rates. This question was raised repeatedly across the workshop but remained open, largely because of a lack of data on movement ecology and population structure in the southern North Sea. It was noted that the body condition work presented by Eva Schotanus (section 3.3.1) showed regional differences in the seasonal variation of body mass index for both juveniles and adults, which casts doubt on the assumption of a single, homogeneous North Sea population. The question of population structure is therefore closely linked to the topic of regional demographic rates: if rates do differ between regions, then both the demographic parameterisation and the density-dependence assumptions (see below) would need to be revisited.

In terms of follow-up actions (Workshop brainstorm output), determining whether population substructuring exists in the North Sea – through tagging, genetics and morphometrics – was placed in the mid-term category (B, until end of 2027), as was region-specific modelling. Investigating potential subpopulations through genetics and (skull) morphology was also identified as a longer-term goal (C, >6 years). Testing the model with subpopulation-specific fertility rates was raised as a near-term (A) idea, albeit with the caveat that the reliability of those rates (derived from different sources such as bycatch and strandings) remains uncertain.

2. Effect of age on resource foraging efficiency ('age at independence')

Currently the effect of age on resource foraging is defined by two parameters: γ and T_r . These parameters take account of the fact that newly weaned calves will not be 100% efficient at foraging and that, for species with long lactation periods, calves may begin feeding during lactation. Currently in the model, the shape of the relationship between calf age and foraging efficiency is controlled by the age at which a calf achieves a foraging efficiency that is 50% of an adult (T_r), and a shape parameter (γ) that determines how rapidly foraging efficiency approaches 100% (Figure 12-1). This relationship is parameterised and the sensitivity analysis of the model showed that the model results are sensitive to the shape of this relationship.

How it was addressed at the workshop: This topic was discussed under the 'Lactation and calf survival' part of Lonneke IJsseldijk's life history talk (section 3.1.1 of Heinis et al., 2026). It was explained that the age at which a calf becomes completely independent of its mother and must find its own food ('age of independence') is determined by the amount and quality of the mother's milk and, at a later stage, by how efficiently the calf can find and catch good-quality prey of its own. In the iPCoD DEB model the related parameters are the age at which a calf's foraging efficiency reaches 50% of the adult level (T_r) and the calf age at which the female begins to reduce milk supply (T_n). It was stressed that milk quality varies in lipid content (probably also with the reproductive state of the female) and may also carry persistent organic pollutants with potential negative effects on calf survival, so that age at independence is unlikely to be a fixed number and would be better represented as a probability or a distribution. This is consistent with the report's sensitivity analysis, which shows model results to be sensitive to the shape of the age-to-foraging-efficiency relationship.

A practical way forward suggested at the workshop is to assess lactation and neonatal diet from post-mortem examined individuals; zooming in on necropsied porpoises of less than 120 cm and assessing their diet could give more clues on age at independence. Lonneke IJsseldijk is considering how best to obtain such data. A recurring obstacle that was discussed is that information on milk content in the stomachs is not always collected as a standard procedure by the different necropsy groups around the North Sea, which limits the comparability and availability of the data needed to parameterise this part of the model. In the brainstorm for future work, determining the age of independence for harbour porpoise calves from necropsies and diet studies was placed in the mid-term category (B, until end of 2027), and quantifying when juveniles become energetically independent (including prey size and success rate as a function of age class) was also identified there.

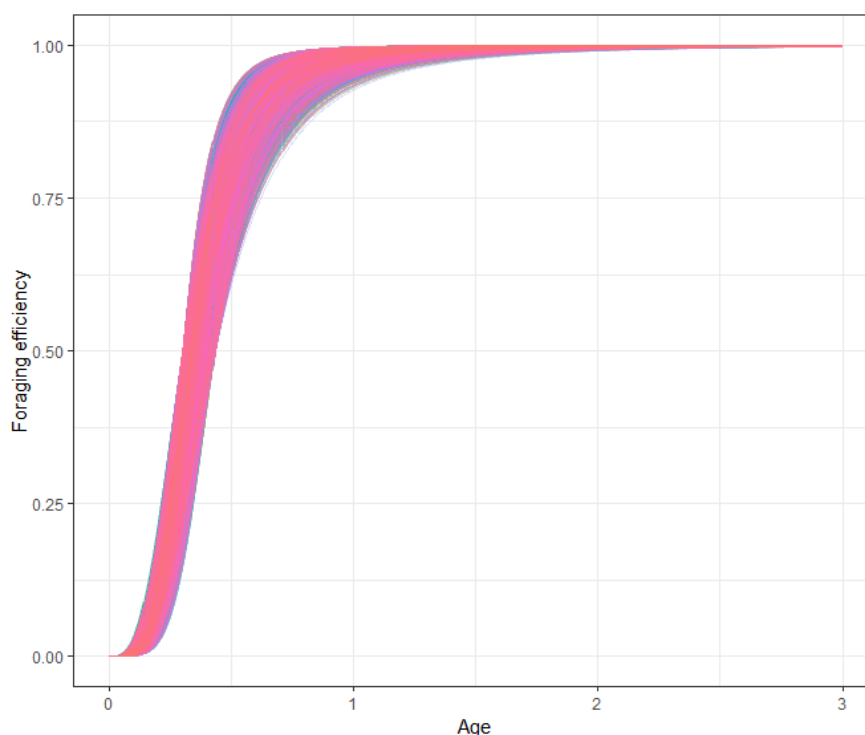


Figure 12-1. Relationship between harbour porpoise age and foraging efficiency for 300 simulations of iPCoD DEB (lines). Foraging efficiency = 0 means that calves are 100% dependant on milk provision from mothers, foraging efficiency = 1 means that calves are not dependant on milk provision from mothers but 100% dependant on other food.

3. How long animals stop foraging when disturbed and can they compensate

The model assumes that animals stop foraging for a defined time as a result of disturbance. The current default value is 6h of no foraging. Results from this project and a previous study (Chudzińska et al. 2024) show that the model results are largely affected by this assumption.

How it was addressed at the workshop: The energetic basis for how disturbance affects body condition was covered in Ron Kastelein's talk on harbour porpoise energetics (section 3.2.1 of Heinis et al., 2026), and in particular his summary of the 24-hour fasting study (Kastelein et al. 2019b). That work, conducted in a controlled environment, showed that the susceptibility of porpoises to a reduction in foraging is seasonal: body mass loss of roughly 4% of body mass occurred per 24 hours of fasting in every season, blubber thickness was reduced by 0–3 mm per 24 hours, and the greatest mass loss occurred in autumn and the least in summer. The conclusion was that harbour porpoises are most susceptible to the effects of fasting due to disturbance in autumn, and that body condition should always be considered in relation to season. A companion study (Kastelein et al. 2019a) showed that if suitable prey is abundantly available after a period of fasting, porpoises can eat a large proportion of their daily energetic requirement in a single feeding bout, refilling the forestomach about 2.5 hours later – a key observation for the question of compensation.

Laia Rojano-Doñate's presentation (section 3.2.2) added evidence from wild, tagged animals. Because harbour porpoises maintain a high field metabolic rate regardless of behaviour and spend a very high proportion of their

time foraging on many small, low-calorie prey items, they are particularly vulnerable to lost foraging opportunities. Recent (under review) results from 28 tagged wild porpoises indicated that, for an average 60 kg animal, 11 vessel events per day resulted in a 4.6% net energy loss per day – equivalent to 10–12 kg of blubber over a year. The implications of such an offset depend on the animal's ability to compensate, the time available and quality of the environment, and its health and reproductive status, with nighttime exposures being especially costly because porpoises forage predominantly at night.

The ability to compensate for lost foraging was widely discussed and emerged as one of the most important and least well-constrained factors. The general discussion on energetics (section 3.2.3) stressed that energy acquisition is very sensitive to the energy content of prey items (the difference between a 4 cm and a 5 cm fish is large) and that, while porpoises burn energy fast, they also appear to recover fast (estimates of around 1 kg per day), although digestive efficiency under rapid refeeding is probably not optimal. The clear message was that the model's treatment of foraging cessation and compensation should, where possible, be revisited and based on more empirical data rather than on parameterised assumptions, given how strongly the results depend on the assumed duration of disturbance (the current default being 6 hours of no foraging).

These energetic findings were brought directly into the modelling context in Magda Chudzinska's talk (section 4.6). She explained that the actual disturbance effect is determined by factors such as the baseline foraging duration and the swimming (fleeing) speed: the longer the baseline foraging duration and the slower the animals swim, the larger the disturbance effect, and these effects vary with the distance of the animals from the piling activity. A central point relevant to this topic is the treatment of compensation in iPCoD DEB: compensation for lost energy intake only begins the day after disturbance, even if piling lasts only 2–3 hours, so no within-day compensation is included. This is a worst-case assumption, and it was suggested that an extra ~5% energy cost for the additional swimming/fleeing activity could also be considered. It was noted that, unlike iPCoD EE, iPCoD DEB can replace the fixed 6-hour disturbance with a distribution around a mean value (see the results of the sensitivity of the iPCoD DEB model to the value for duration of foraging cessation in section 4.3), and that because each female builds up a calendar of disturbance events, the timing and clustering of disturbance days (and hence the piling schedule) strongly influence the outcome. In the brainstorm for future work, achieving a better understanding of how long it takes to recover from disturbance (and quantifying the 'time to first buzz' as a function of individual context) was placed in the near-term category (A, 0–3 months), while several tag-based and experimental studies on the severity of response and digestive efficiency were placed in the mid-term category (B).

4. Seasonal changes in body condition

Currently in the model, the timing and frequency of the piling operations in relation to the annual reproduction cycle may have a large effect on the population dynamics. This is because females' body condition changes largely during the year and their response to disturbance is, therefore, largely linked to their body condition.

Question posed at the workshop: Is the model parameterised to the best available knowledge on seasonal changes in body condition?

How it was addressed at the workshop: Seasonal changes in body condition were a recurring theme and were covered most directly in the body condition and health session (section 3.3 of Heinis et al., 2026), particularly in Eva Schotanus's presentation (section 3.3.1). Measurements on around 1,700 stranded porpoises from six regions around the North Sea and the northern English Channel demonstrated regional differences in the seasonal variation of body mass index (BMI) for both juveniles and adults. The energetics talks reinforced this: Ron Kastelein (section 3.2.1) concluded that body mass, blubber thickness and food consumption all vary seasonally with water temperature, and Laia Rojano-Doñate (section 3.2.2) showed that porpoises cyclically change their blubber thickness by around 10 kg over a year. The discussion highlighted that the threshold at which animals die is very different depending on natural environmental conditions, and that porpoises in the warmer southern North Sea can afford a lower blubber thickness than those in the north. The overall sense was that the model captures the existence of strong seasonal variation, but that the regional dimension of that variation – and the implication that resilience may not be uniform across the North Sea – is not yet reflected. Modelling the effect of sea surface temperature on health parameters such as blubber thickness and prey consumption and implementing a cost of thermoregulation as a function of blubber thickness and temperature, were both identified as model-extension actions (the latter in the near-term category A, the former in B).

5. Starvation-induced mortality rate

This parameter determines how long an individual is likely to survive if its body condition falls below the starvation body condition threshold (ρ_s). Currently this parameter is parameterised in the model and varies between 0.13 and 0.24 depending on time of the year.

Question posed at the workshop: Can necropsies provide a more updated value?

How it was addressed at the workshop: This topic was addressed in the presentations by Andrea Gröne on diagnosing emaciation versus starvation (section 3.3.2 of Heinis et al., 2026) and Andrew Brownlow on physiology and pathology (section 3.3.4). A key outcome was the recognition that modellers and pathologists currently use different terminology for the same terms. Pathologists distinguish emaciation (a long-term, chronic process, with very thin blubber and often other disease findings) from starvation (an acute, quick process, sometimes in animals with decent blubber and reserves, and often in newborns), and they rarely record 'starvation' as a cause of death, instead identifying some other proximate cause. For the modellers, by contrast, starvation is a physiological point of no return – a state from which an animal cannot return to a healthy body condition – and what matters for the model is the animal's condition and how disturbance affects it, not how it ultimately died. The discussion (section 3.3.3) concluded that the model terminology is potentially confusing and that a clearer term, or a very clear definition, is needed so that necropsy data can be compared and used as model inputs.

Andrew Brownlow's presentation set out the physiological cascade towards end-stage debilitation and death (from primary feeding impairment, through acute metabolic response and physical degradation, to parasitic amplification), and made the important point that an external body assessment may not be sufficient to predict survival: animals with excellent reserves can die from an acute negative energy balance within 24–48 hours, while chronic disease burden can render animals vulnerable to otherwise survivable stressors. This has a direct bearing on the starvation mortality rate parameter, which determines how long an individual is likely to survive once its body condition falls below the starvation threshold. The workshop suggested that necropsy data could, in principle, provide more up-to-date estimates of the target body condition of adults and calves, the starvation body condition threshold, and the starvation mortality scalar/rate, but that doing so requires harmonised diagnosis across stranding networks. Working towards a consensus on the diagnosis of starvation as a cause of death (and reassessing existing cases), and harmonising pathology terminology, were both placed in the mid-term category (B, until end of 2027) in the brainstorm for future work.

6. Probability of exposure, probability of disturbance

In both iPCoD EE and iPCoD DEB, the number of animals affected by piling noise is estimated from the probability that an individual is present to be disturbed (probability of exposure) and the probability that, once present, it responds (probability of disturbance). For KEC 5.0 these were derived by calculating the number of animals within the area where the Sound Exposure Level exceeds the behavioural-response threshold and applying a sound dose-response curve, with local density taken from the Gilles et al. (2020) distribution map.

How it was addressed at the workshop: This topic was addressed in the talk on key factors for modelling the effects of disturbance by Cormac Booth and colleagues (section 4.5 of Heinis et al., 2026), and again in Magda Chudzinska's talk (section 4.6). It was stressed that establishing the probability of disturbance depends heavily on movement ecology, and in particular on whether the population is assumed to be resident or nomadic: in a nomadic population many individuals are disturbed relatively infrequently, whereas in a resident population fewer individuals are disturbed frequently. Because iPCoD simulates over 20–30 years, the assumptions about animal movement need to be robust over that timeframe. An overview of the available tagging data showed large individual variation in the area used and distance travelled, evidence of both extensive movements and strong site fidelity, and – critically – that movements of harbour porpoises in the southern North Sea are essentially unknown. The contrast with DEPONS was drawn out: DEPONS is an individual-based model in which repeated exposure is explicitly modelled because each animal has its own movement history, which is not possible in the iPCoD models. In iPCoD DEB, every individual in the (sub)population is currently assumed to be equally susceptible to exposure, although each female does build up a calendar of disturbance events. The discussion concluded that movement ecology dictates both exposure and effect, and that improving the understanding of harbour porpoise movement in the southern North Sea is a priority. Improving movement patterns, quantifying cumulative exposure using agent-based (IBM) models, and extracting the probability of repeated exposures from DEPONS were all placed in the mid-term category (B, until end of 2027) in the brainstorm for future work.

7. Field metabolic rate

The Hin et al. (2019) model assumed that an individual's Field Metabolic Rate (FMR) is a simple multiple of the Resting Metabolic Rate (RMR) predicted by the Kleiber (1975) relationship. This multiplication was parameterised in the model and the value chosen has a large effect on the results. FMR is also highly linked to the resource availability parameters (Rmean). Currently a multiplier of 4.5 – 5.8 (called Sigma_M) is used in the model but these values vary depending on the resource availability. As presented in section 4.4, if the effect of environmental stochasticity is included, these two parameters (Sigma_M and Rmean) have a large impact on model results.

How it was addressed at the workshop: Field metabolic rate (FMR) was not included as a dedicated discussion topic at the workshop, in the end, due to lack of time. It was, however, touched on indirectly in the energetics presentations: Laia Rojano-Doñate (section 3.2.2 of Heinis et al., 2026) reported a high FMR of approximately 20 MJ/day with little seasonal variation, maintained regardless of behaviour, which is precisely the feature that makes porpoises vulnerable to lost foraging opportunities. Although FMR itself was not debated as a parameter, the brainstorm for future work did identify several actions that bear directly on it and on the strongly linked resource-availability parameter (Rmean). In particular, refining the energetics model using data from captive porpoises (weight, body mass, growth, prey intake, reserve dynamics, metabolism and energy density of prey) was listed in both the near-term (A) and model-testing categories, and conducting controlled studies on food composition and body weight, including the partitioning of ingested energy between locomotion and thermoregulation, was placed in the longer-term category (C, >6 years). These would provide the empirical basis for revisiting the BMR multiplier (Sigma_M) and its interaction with resource availability in a future model update.

8. The effect of density dependence on demographic parameters

The model includes the relationship between available resources and population size (density dependence). This relationship between available resources and population size was extracted from a harbour porpoise DEB model by Hin et al. (2021), where density dependence is an emergent property of this model because resource density increases if the population falls below its equilibrium level, resulting in an increase in individual survival and birth rates.

Question posed at the workshop: Is this link based on best available knowledge? And how should it be modelled if demographic parameters differ between North Sea regions (see point 6).

How it was addressed at the workshop: Density dependence was mentioned in several places but was not concluded as a separate topic, largely due to a lack of data. It was discussed most explicitly within Magda Chudzinska's talk (section 4.6 of Heinis et al., 2026), where the mechanism was set out: the relationship between available resources and population size, extracted from the Hin et al. (2019) harbour porpoise DEB model, works

through food availability, so that a reduction in population size is assumed to increase resource density and thereby increase calf survival and fertility. An important caveat raised at the workshop is that this assumes any increase in prey density would be available to all individuals in the porpoise population, which may not hold because there are many other generalist predators in the North Sea competing for similar prey; as a result, the speed with which the population returns to its equilibrium is probably overestimated. The discussion also linked density dependence back to the open question of regional differences in demographic parameters (see the topic on demographic rates above): if rates differ between North Sea regions, then how density dependence should be modelled becomes more complex. In the brainstorm for future work, studying the effect of different types of density dependence on the population response to disturbance was identified as a model-extension action in the mid-term category (B, until end of 2027).

Conclusions from Appendix C

The workshop confirmed that several of the parameters identified as candidates for review are indeed both influential on model outputs and currently constrained largely by parameterisation rather than direct empirical evidence. A number of cross-cutting themes emerged across the individual topics.

First, the question of whether harbour porpoises in the North Sea constitute a single population or several (sub)populations recurred throughout the workshop — in the life history talks, the body condition work, and the discussion of movement ecology — but remained unresolved for lack of data. This question is foundational, because it bears directly on whether region-specific demographic rates are needed, how density dependence should be represented, and how the probability of exposure should be modelled. Closely related is the consistent evidence for regional and seasonal variation in body condition, which the model captures in its seasonal dimension but not yet in its regional one.

Second, the ability of animals to compensate for lost foraging, and the related assumption about how long animals stop foraging when disturbed, were identified as among the most important and least well-constrained elements of the model. Because results are strongly sensitive to these assumptions, there was broad support for revisiting them on a more empirical basis as data become available. The flexibility of iPCoD DEB — its ability to represent a distribution of disturbance durations and an individual disturbance calendar — was recognised as an advantage over iPCoD EE in this respect.

Third, the movement ecology of harbour porpoises in the southern North Sea was repeatedly identified as a critical knowledge gap, since it underpins the probability of exposure and the treatment of repeated disturbance over the 20–30 year simulation horizon.

Fourth, a recurring practical message was that a considerable amount of relevant information already exists in stranding and necropsy data, but that realising its value for the models requires harmonised diagnosis and terminology across stranding networks, and clearer communication between modellers and pathologists — most visibly around the definition of "starvation".



The mapping of ideas for future work nevertheless placed concrete follow-up actions against most of these topics across the near-term (A), mid-term (B) and longer-term (C) horizons, providing a route by which the priorities identified here can feed into successive KEC updates.